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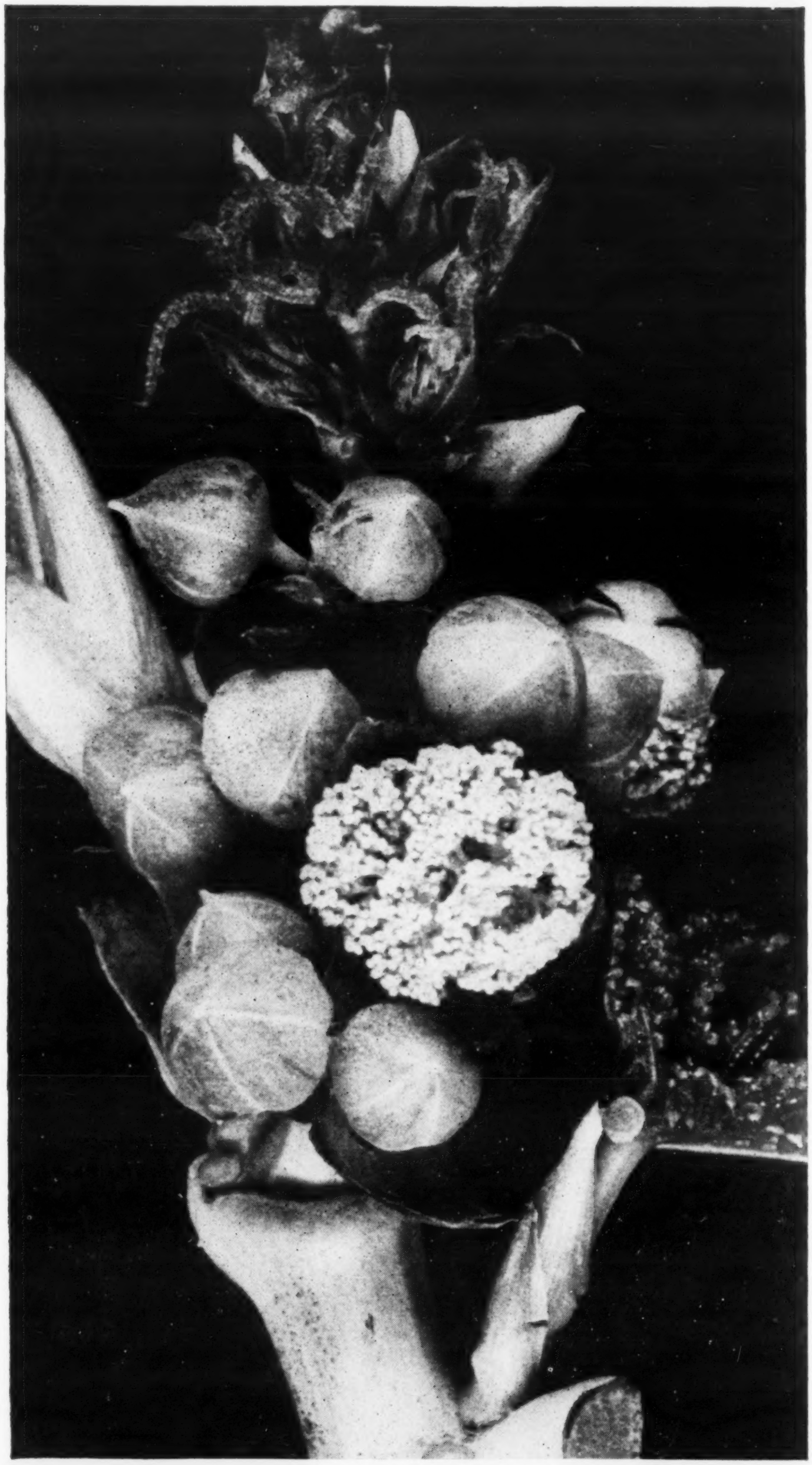


MALE AND FEMALE FLOWERS OF THE CASTOR BEAN

The rough horn-like stigmas of the female flowers are shown at the top of the flowering spike. The buds on the lower portion of the spike are those of male flowers. Only one male flower in full bloom is shown. (Slightly magnified.) (Frontispiece.)

BREEDING NEW CASTOR BEANS

Castor Oil Now Becoming of Immense Commercial Importance as Motor Lubricant—Careful Breeding of Varieties Having Desired Attributes Necessary to Produce Best Commercial Seed—Many Characters Show Mendelian Behavior.

ORLAND E. WHITE

Curator of Plant Breeding, Brooklyn Botanic Garden, Brooklyn, N. Y.

THE well-known castor oil is expressed from the seeds of a Euphorbiaceous ornmental plant (*Ricinus communis*), related to our scarlet poinsettias. Hundreds of distinct varieties of this plant are known in the tropics—especially in India, where the bulk of the world's crop is grown. Most treatises roughly divide these numerous varieties into large and small-seeded types, the former producing supposedly less oil and of inferior quality. A collection of several hundred types (see Figs. 1 and 2), commercial and otherwise, assembled from various tropical and sub-tropical regions, discloses the fact that no sharp line can be drawn between the large Zanzibar types, running 450 to 600 beans per pound, and the small Bombay beans, running anywhere from 1,500 to 4,500 beans per pound, depending on the variety. All degrees of intergrades in size of beans exist, these, no doubt, resulting from more or less chance crossing, which wind and insects have brought about during the centuries of its cultivation.

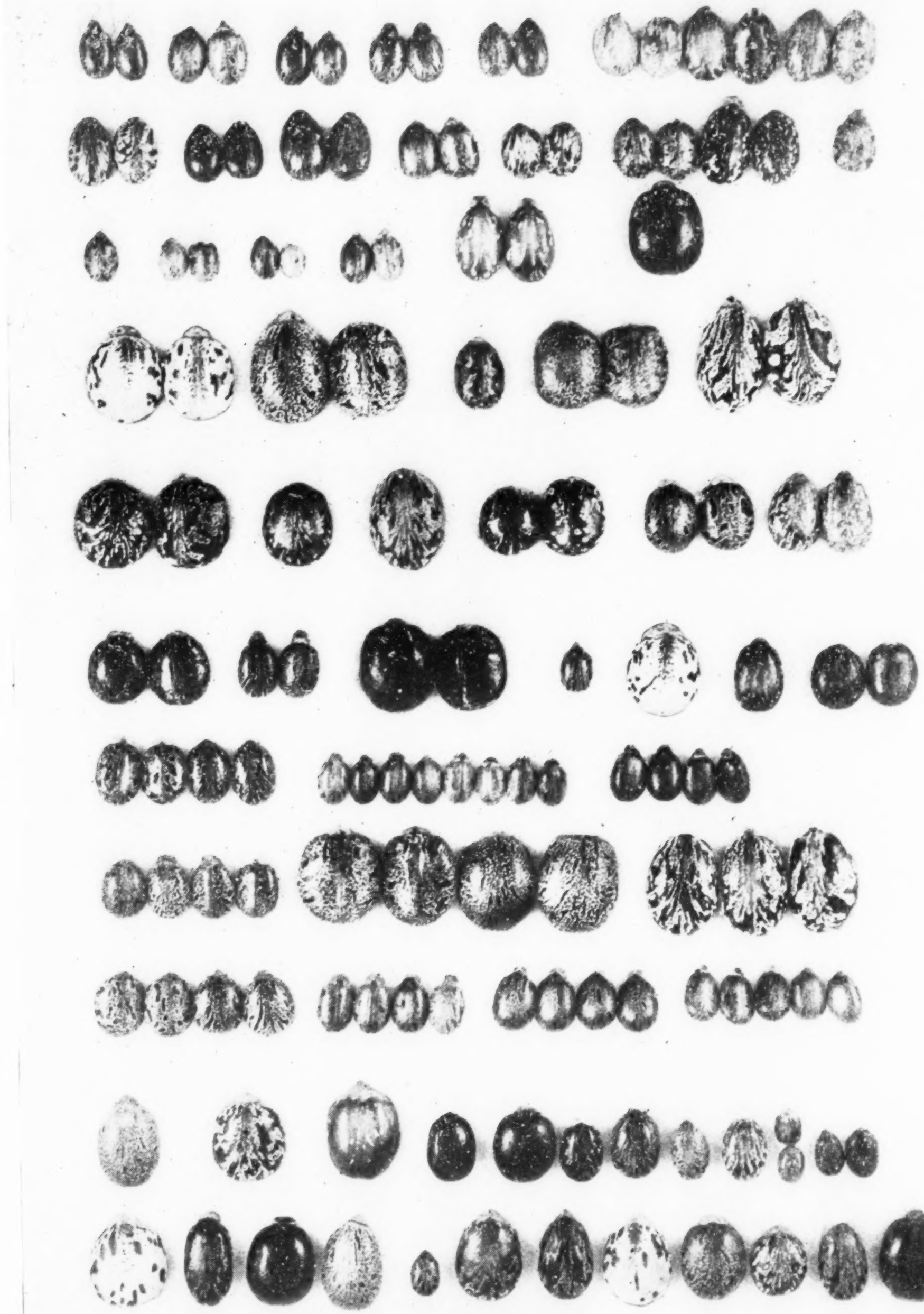
BEANS MAINLY IMPORTED FROM INDIA

Of the million or more bushels of beans annually imported into this country through the port of New York, the bulk come from Madras and Bombay; a few from Mexico, Brazil, Argentine Republic, Java, and China. The Indian beans as they reach our factories are generally a mixture of such small and medium seeded types as are represented in Fig. 2. The large seeded types, shown in the same figure, were said to be Chinese and are grown considerably in Mexico. The oil content of the Indian beans runs as high as 55 per cent, while the large Zanzibar beans give only 35 per cent oil, and of inferior quality because of the increased amount of "acid." Shortly after the Civil War, castor oil bean farming in the United States became a promising local industry in Kansas, Illinois, and other Middle Western States, but overproduction and competition with cheap Hindu labor soon made it unprofitable. Castor oil beans, as late as twelve years ago, were raised commercially in Oklahoma, and the scarcity of imported beans and the increased demand for the oil, due to the war, will probably bring large areas in these sections again into castor oil bean cultivation. Large sandy areas in the Gulf States, now largely waste land, are said to be eminently fitted for this crop. The crop runs anywhere from 10 to 40 bushels per acre, depending largely on the variety planted, the soil, the climate, and the length of frostless season. Even as far north as Iowa, from 15 to 25 bushels per acre have been obtained.

The oil has innumerable uses, chief among these being its value in dyeing cloth, in medicine, and as an aeroplane motor lubricant. Its non-drying, non-gumming properties, and its high density are said to make it especially desirable for lubricating the newly invented Liberty motor. Normally this country uses about 1,000,000 gallons annually, but the war and the increased use of aeroplanes after the war probably will many times increase this amount.

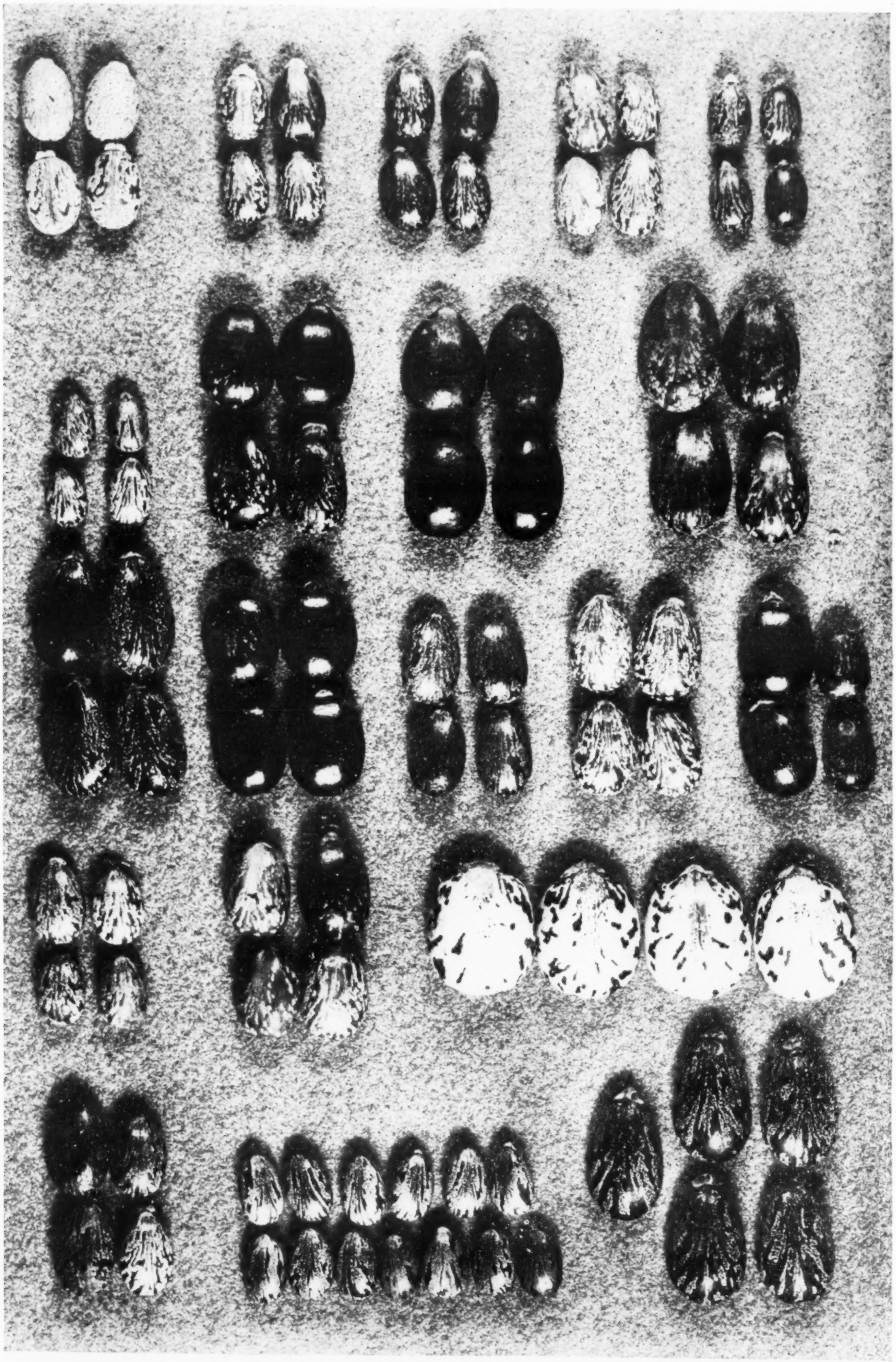
BREEDING OF GOOD TYPES ESSENTIAL

To make commercial castor oil bean growing in this country a permanent industry, requires the breeding of varie-



VARIATION IN SIZE, SHAPE, PATTERN, AND COLORING

Each group in all but the last two rows represents a distinct kind or variety. Often the beans are arranged to show upper and lower surfaces. The very large beans are Zanzibar types with low oil content. In the last two rows, each variety is represented usually by a single bean. These beans are types from Mexico, Italy, Java, Zanzibar, Uganda and Rhodesia. (Reduced one-third.) (Fig. 1.)



COMMERCIAL TYPES OF CASTOR BEANS

Each of the groups represents one type. The first three rows represent commercial types of India. The last two rows are types from Mexico, Java, British West Indies and India. (Natural size.) (Fig. 2)

ties with the highest possible oil content, the smallest amount of the objectionable "acid;" varieties adapted to such waste lands as those of the sandy areas of the Gulf Coast and other sandy regions of the southern United States, and, perhaps, the sandhills of Nebraska; varieties having close, compact, fruiting spikes with thin-walled, spineless, "non-popping" seed capsules. The plants should be prolific in fruiting spikes, early maturing, and bear over a long season. The materials for producing such varietal types already exist among the innumerable forms of castor beans, the main problem being to bring them together into one or more commercial varieties.

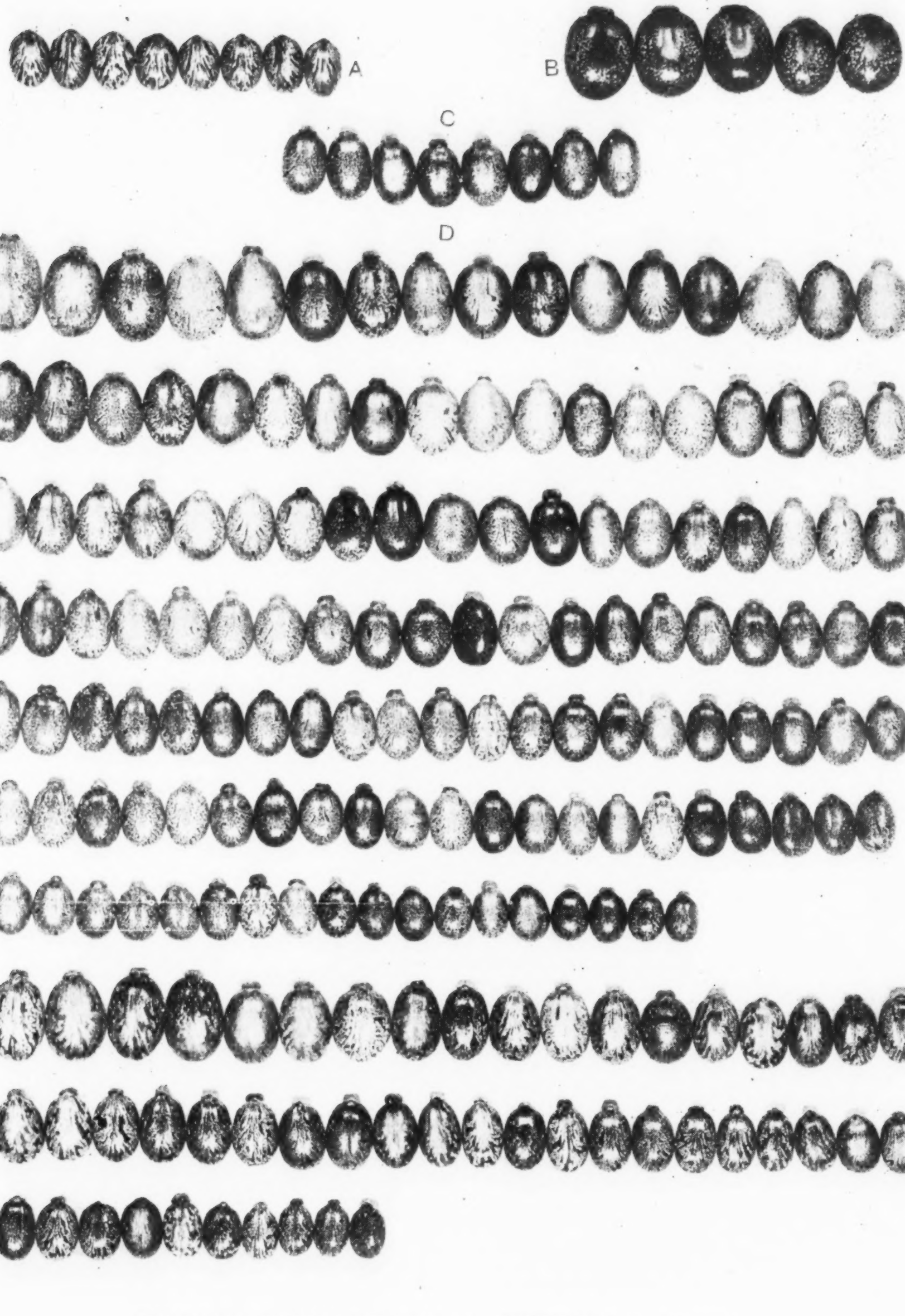
So far as the writer knows, no very serious attempt has been made to do this, although some plant-breeding work and variety testing has been done in Algeria, British West Indies, Egypt, and India. From several years experience, the writer has found the castor oil plant an excellent subject for plant-breeding work. The plants are easily grown, comparatively free from disease, the seeds remain viable for several years with a very high per cent of germination. All the types, even to the most extreme, readily cross, giving fertile F_1 and F_2 hybrids. Some varieties when crossed, give a much larger yield of seed in the F_1 generation, while of other types, as in maize, this is not true. Among the characters showing Mendelian behavior are stem, foliage, and seed coat color, glaucous or non-glaucous plants, "popping" or "non-popping" seed capsules (dehiscent or indehiscent), types of seedcoat mottling, seed size and shape, height of plant, compactness and size of fruiting spike, time of maturity, certain leaf characters, etc. Only a few of these characters have been studied in enough detail so that they may be placed on a factorial basis. Such a character as indehiscent capsules, when combined with thin capsular walls and other characters should be especially valuable in a variety grown for oil, since a large per cent of the seeds are not wasted by the popping of the mature capsules. Also labor is saved, since it is not necessary to harvest the crop once or twice a week in order to avoid loss, as is the case with common popping varieties. This characteristic is easily transferred as apparently not more than two pair of factors are involved.

PLANT IS MONOECIOUS

As is well known, the castor bean plant is monoecious, the male and female flowers appearing on different portions of the same flowering spike (see Frontispiece). Both types of flowers mature at about the same time, the male flowers perhaps slightly earlier. All the flowers, either male or female, of the same spike, do not mature at the same time. The proportion of female flowers destined to produce mature capsules, usually involve a week or so in setting so that the seeds of one spike ripen at about the same time. Square bottomed, light colored manila paper bags are used to cover the inflorescence when selfed seed is desired or when crosses are made. The sacks should be of fair size, as it may be desirable to keep the rapidly lengthening inflorescence covered for a considerable period, until all danger of "adventitious" female flowers appearing and contamination resulting thereby, has been eliminated. After bagging, when selfed seed is desired, the bags should be shaken every few days as the pollen matures, so as to insure plenty of "fruit" setting. In a windy country this may not be necessary, but the writer finds it to be so in his work in Brooklyn.

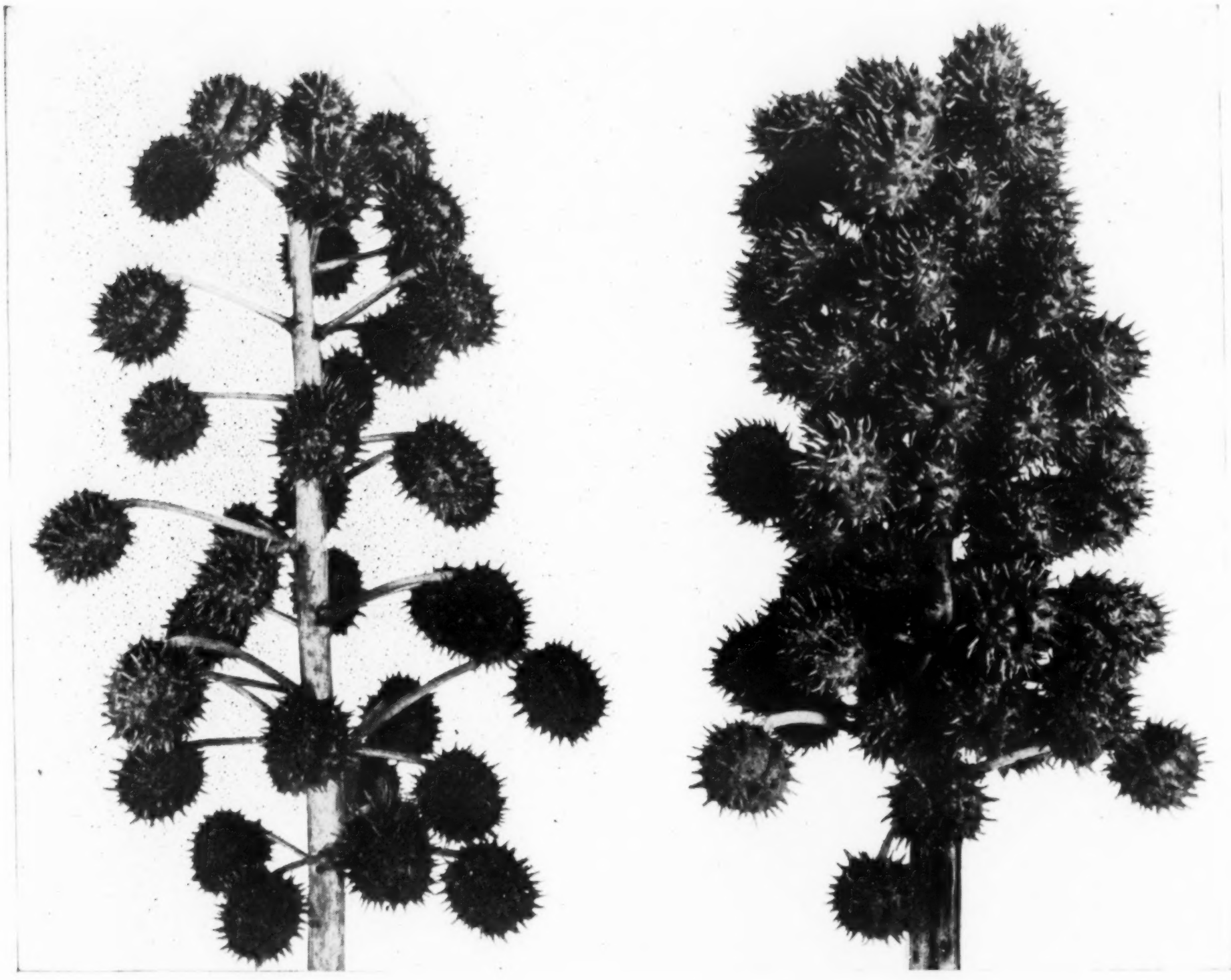
GENERALLY BREED TRUE

Observations based on cultures in the breeding plots at the Brooklyn Botanic Garden show that many of the varieties, much to my surprise (since the castor oil plant is monoecious and wind-pollinated), breed true to many of their most prominent characters immediately. Data from progeny of plants of different varieties, grown close together, indicate that very little cross-fertilization took place (probably not more than 5%), even when conditions appeared most favorable. This may be accounted for, perhaps, by the copious supply of pol-



RESULTS FROM CROSSING DIFFERENT TYPES

Illustrates inheritance of seed dimension and coarse and fine seedcoat mottling. A. Maternal parent. B. Seeds in all respects similar to paternal parent. C. F_1, progeny. Note the uniform appearance both as to size and mottling the F_1, progeny seeds. D. F_2, in progeny. The coarse and fine mottled segregates are arranged in a separate series. In every case, each single bean represents a typical bean from one plant. (Reduced one-third.) (Fig. 3.)



LOOSE AND COMPACT FRUITING SPIKES

The types with compact spikes in general are greater seed producers, and hence of more commercial value. (Fig. 4.)

len of the male flowers, the comparative proximity of the female flowers, and the sheltering effect of the foliage against air currents bearing foreign pollen. The flowers are said to be excellent honey producers for bees, so where these are common one might expect a much greater amount of cross fertilization.

In selection work, such as the isolation of high oil producing types, it seems best and most practical to insure complete isolation by using paper bags as mentioned above. In making crosses, the male flowers may be easily removed without harming the spike and the remaining female flowers. Male flowers usually mature and shed their pollen in early morning. The pollen remains viable for at least a week, when kept in a dry place.

Breeding Sows Before Litters are Weaned

Experiments described in the monthly *Bulletin* of the Ohio Agricultural Experiment Station for May, 1918, would indicate that there is no danger in breeding sows when their litters are from 43 to 56 days of age. Conception seems to take place just as readily, the milk flow is apparently not affected and the pigs seem to thrive just as well as if breeding did not take place until the litter was weaned.

GIRDLING THE CORINTH GRAPE TO MAKE IT BEAR

The Zanth Currant Industry in California—An Early Seedless Raisin Crop—Yearly Girdling at Proper Time Secures Large Crop and Superior Fruit

GEO. C. HUSMANN

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BECAUSE there is a bush fruit grown called currant, many people imagine that the dried grapes used so extensively in cakes, puddings, etc., are the dried fruit of the currant bush (Ribes species), when, in reality, the currants of commerce are dried grapes.

According to Eisen, they are referred to by Pliny as being grown in Greece in 75 A. D., after which there appears to be no further historical record of them for nearly a thousand years. During the eleventh century, in the old herbals and in the literature of the fourteenth, fifteenth, and sixteenth centuries, references to them occur as "reysyns de corauntzs," "Corauntz," "Corent," "rey somys of Corawnce," "raysns of Coren," and "currans."

The name currant appears by gradual evolution to have developed from the name Corinth, the port from whence the early supplies of this fruit reached western Europe, furthermore the currant grapes were heard of 1,600 years before, and the name "currant" or "currantes" was applied to these grapes as early as 1578, several centuries before the common garden currant was first cultivated late in the sixteenth century.

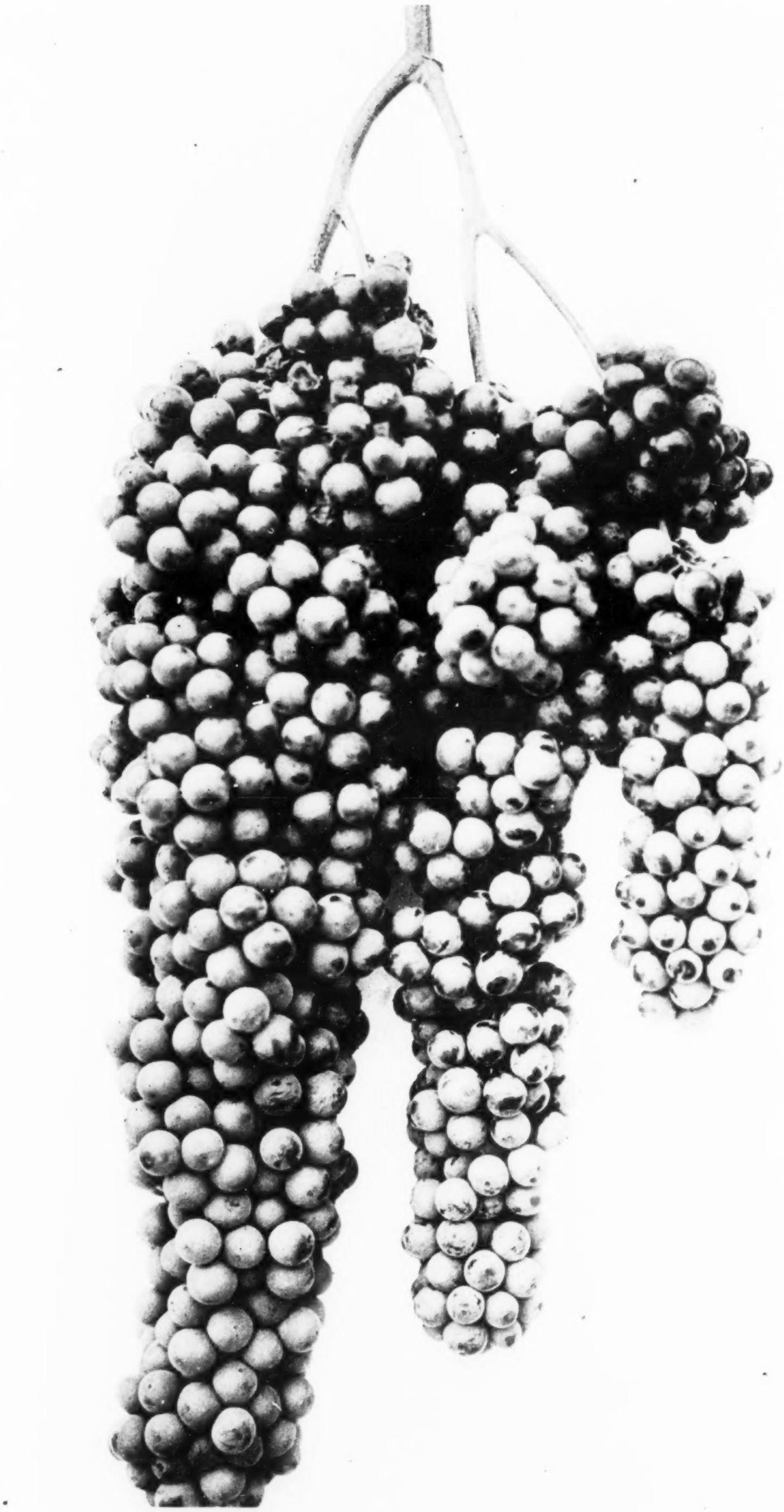
HISTORY OF THE CURRANT GRAPE

The following, relative to the importance of the currant grape industry in Greece, will prove interesting.

The destruction of the vineyards in France by phylloxera during the middle of the last quarter of the last century, caused a heavy demand at high prices for dried currants for use in the making of wine, brandy, etc. This resulted in the planting of so large an acreage of such grapes in Greece, that in some regions it became the sole industry.

The reestablishing of the French vineyards on phylloxera resistant grape stocks introduced from the United States, and France in 1896 and the imposing of import taxes on dried currants practically excluded them from France. This resulted in a serious crisis in the currant industry of Greece, the production of them being far in excess of the demand.

The "parakratesis" or "retention" act was passed by the Greek Parliament in 1895, for the purpose of maintaining prices and controlling the yearly output, and to prevent as far as possible, the overstocking of the markets. This law imposes on the producer a tax of 15% of the currants he exports, payable either in money or by deposits of the required quantity of currants in the government warehouses. The currants received by the government must be put to other than the usual uses made of them. This tax is one of the principal sources of revenue of the Grecian government. In connection with the passing of the retention act the establishing of the "currant bank" of Greece was agitated to enable producers depositing a certain quantity of currants in a government warehouse, either to draw money from



EFFECT OF GIRDLING ON THE CURRANT GRAPE CLUSTER

This cluster of the Panariti grape was borne by a vine of which the trunk had been girdled at blossoming time. The stock is Ruprestris St. George. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 5.)

CLUSTER FROM UNINCISED GRAPE VINE

Panariti cluster from unincised vine on Rupestris St. George. Fresno Experiment Vineyard.
(Fig. 6.)

CURRANT GRAPE CLUSTERS FROM GIRDLED AND NOT GIRDLED VINES

On the left a saleable cluster of Panariti grape from a vine which was girdled at blossoming time. On the right three imperfect unfilled clusters from not girdled vines, showing their unsatisfactory character. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 7.)

such bank or to hypothecate their crop. Such a bank was finally established in 1899, with a capital of 300,000 drachmas (about $675,500), realized by the government from the sale of currants to distillers, etc. The United States, previous to the war, annually imported over 30,000,000 pounds of such dried currants the equivalent of 100,000,000 pounds or 50,000 tons of fresh grapes, as it takes about three pounds of fresh grapes to make one pound of dried.

CAN BE PROFITABLY GROWN

The United States Department of Agriculture has succeeded in demonstrating that these currant grapes can be profitably grown in America. This paves the way for the establishment of another very important and extensive grape industry in this country. Another exceedingly important matter is that the currant grapes are among the very earliest grapes to ripen, in fact, ripen so early that they will be dried and put away before the earliest rains occur in districts where other raisin varieties are too late in ripening, and in the present raisin sections of this country currants can be grown as an advance crop and be cured and stored by the time other raisin grapes ripen, so the same labor employed in harvesting and curing currant grapes can, after having accomplished that work, harvest and cure the other raisins.

Currant grape varieties were introduced into California as early as 1861, and these were followed by later introductions. Among all these, however, there appears to have been no valuable dark colored varieties, but some fairly productive red and white strains producing fruit of inferior quality.

The "Panariti" was introduced by the

GIRDLED CURRANT GRAPE VINE CARRYING FORTY-ONE POUNDS OF FRUIT

Photograph taken at ripening time of a Panariti currant grape vine grafted on the hybrid stock Aramon x Rupestris Ganzin No. 1. A ring of bark one-half inch wide was removed from the canes at blossoming time, two months previous to ripening time of the grapes. Compare with photograph of ungirdled vine carrying only twenty-one pounds of poorly formed clusters. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 8.)

United States Department of Agriculture through Mr. David Fairchild, Agricultural Explorer of the Department, a consignment of cuttings of them reaching Washington, D. C., May 9, 1901. Concerning this Mr. Fairchild stated at that time: "The variety of grape producing the currants or corinth of commerce. These cuttings were purchased in the village of Panariti, which lies among the mountains back of Xyloncastron. This village is noted as producing some of the finest corinths in Greece."

Several currant grape varieties are grown in Greece, though the crop differences are not distinguished in that country as varieties, but by the name of the region in which they are produced.

Some of the Panariti cuttings were distributed to grape growers in California, Arizona, and southern Nevada, and some used in experiments in the Department's Experiment Vineyards in California. Exceptional difficulties were encountered in successfully growing these, and it became a problem for the viticultural investigations of the United States Department of Agriculture to find out where the trouble was. The knotty parts of this problem appear now to have been solved.

Two cardinal points must be observed to grow them successfully, namely, they should be grown grafted on phylloxera resistant stocks congenial to them and suited to the soil and other conditions in which grown, and the vines need to be thoroughly girdled at the proper time.

In a ten-year test of growing them on various resistant stocks, a sufficient number of varieties of these stocks have been found from which to select such as are adapted to any of the soil types as well as to other conditions, and that are furthermore congenial to the currant grape varieties and on which they show good fruiting tendencies.

VINE GIRDLING NECESSARY

It has been ascertained that to make the blooms set and secure a full crop of fruit, the vines must be girdled. This girdling consists in making two parallel incisions through the bark, around either the trunks, arms, or canes of the vines, and taking out the bark between the two parallel cuts. This girdling must be thoroughly and cleanly done, and done while the vines are in bloom. Girdling the vines is not only necessary to promote a full setting and maturing of the fruit, but thereby more than twice as much and a better quality of fruit is obtained.

Vines in the United States Department of Agriculture Experiment Vineyards produced from eighteen to forty-five pounds of fruit to the vine, the crop depending largely on the variety of resistant stock on which the vines were grafted.

When vines are planted 8 x 8 feet apart (the usual distance) an acre will yield a crop of fresh grapes ranging from six to fifteen tons, an average of ten and one-half tons or conservatively from two to five tons of dried currants. From this we conclude that from 4,000 to 8,500 acres of these grapes would be necessary to produce the 30,000,000 pounds we annually import and consume, and, no doubt, the consumption of them could be much increased beyond this.

The berries being seedless, delicious in flavor, rich in quality, and so very early in ripening, they also make an exceedingly desirable fresh fruit for the table.

It is, of course, a great advantage in growing grapes for drying purposes, to be in a district which permits sun drying. All the districts in California, in which grapes for the various purposes are now grown, it appears have suitable conditions for the growing of currant grapes. Protection against the dew at night will likely be necessary in some of the coastal districts, but as it is preferable that the currants, while drying, be shaded during the great heat of the day, the same shelter will do for both purposes.

The importance of the Panariti in the currant group of grapes suggests a description of its fruit. Cluster fairly compact, cylindrical to tapering, long, narrow, usually prominently

NOT GIRDLED CURRANT GRAPE VINE CARRYING ONLY TWENTY-ONE POUNDS OF FRUIT

Photograph taken at ripening time of a Panariti currant grape vine grafted on the hybrid stock Aramon x Rupestris Ganzin No. 1 Not only do the not girdled vines of the Panariti grape bear much smaller crops of small inferior often imperfectly developed clusters, varying in compactness, but on many of them a majority of the berries never develope. This ungirdled vine carried only twenty-one pounds of poorly formed clusters. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 9.)

A GIRDLED CURRANT GRAPE VINE IN FRUIT

A ring of bark one-half inch wide was removed from the trunk at blossoming time two months previous to ripening time of the grape. A callus has formed, partly closing the incision which is still visible in the center of the photograph. The stock is Rupdstris St. George. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 10.)

THE GIRDLE SCAR ON A CURRANT GRAPE VINE

A ring of bark, one-quarter inch wide, was removed from this trunk of a Panariti vine. Photographed (enlarged three diameters) at ripening time, eight weeks after girdling was done. U. S. Department of Agriculture Experiment Vineyard, Fresno, California. (Fig. 11.)

shouldered, often in two parts. Berry very small, usually less than one-quarter inch in diameter, globose, color purple black with whitish bloom, surface smooth; skin thin, tender; flesh pearly white, soft, juicy, seedless. Flavor rich, very sweet and characteristic of the currant grapes. Relatively high in saccharine and acid. Excellent in quality both as fresh fruit and dried. Ripens from July 15 to August 15. Usually produces a small second crop of small loose clusters, of larger seeded berries.

Laboratory Methods Needed in Handling Defectives

Although the fact that mental defectives present a serious problem is now generally recognized, the statement by Dr. Wm. J. Hickson that a group of mental defectives representing feeblemindedness, psychopathy or both which aggregates but two per cent of our population keeps the other group of 98% busy caring for it, crystallizes the matter in a more serious light than many of the 98% realize. Social service work is receiving more and more approval and today prevention is recognized as a most vital part of the work. It is hence necessary that laboratory methods be used in psychiatry, and that vital questions be decided by expert medico-sociologists and not left to passions, prejudice, near knowledge or ignorance. Artificial laws will have to give way to natural laws in dealing with the defective as rapidly as the latter are discovered, and it is only by laboratory investigation replacing hit-or-miss guesswork that a solid scientific basis can be built up for future legislation.

Although environment has an unquestioned influence in molding the individual, there seems to be little doubt that it is extrinsic, while heredity is intrinsic. Daily experience teaches how numerous are those rising above their environment as compared with those sinking below it. After a psychopathologist has examined a case he can very closely approximate not only the family history, but also the past and future history of the case and what the progeny may be. In many cases where environment would seem to be the sole contributing cause to defection, it will be found that it is the inherently defective constitution of the 2% which has given way. It is an interesting fact that but 2% of those contracting syphilis develop parasyphilitic diseases such as tabes dorsalis and paresis. Laboratory methods and investigation may open ways of providing for those of inherently defective constitution, but heredity may well be called the hereditary enemy of medicine.

Effect of War on School Enrollment

Enrollment in American public schools has been affected by the war, but not to the extent of making it less than last year, according to figures compiled by the Department of the Interior through the Bureau of Education. Figures from 1,411 cities and 696 counties or districts show an increase of close to the normal amount of 2½% in elementary schools. In high schools, however, the increase is only one-fourth of the usual 9½%.

Such increase as there is in high school enrollment is caused by the girl students. Fewer boys are enrolled this year in every class in high school except the fourth; apparently there is a healthy tendency for boys in the senior year to remain and graduate.

In city elementary schools the increase in enrollment is actually somewhat above normal; but in city high schools there is a marked falling off, especially among the boys.

Country schools show some gains over last year both in elementary and high school enrollment, but not as great as would be expected under normal conditions. Rural high schools show increases for both boys and girls, despite the war.

PRODUCING BREAD MAKING WHEATS FOR WARM CLIMATES[1]

Introducing the Better Bread Making Quality of Soft Wheat Glutens into the Gluten of Macaroni Wheats—The Opaque Grain Indicates Insufficient Gluten, Translucent Grain an Abundance of It—Microscopic Sections an Aid in Breeding.

GEORGE F. FREEMAN

Department of Plant Breeding, University of Arizona, Agricultural Experiment Station, Tucson, Ariz.

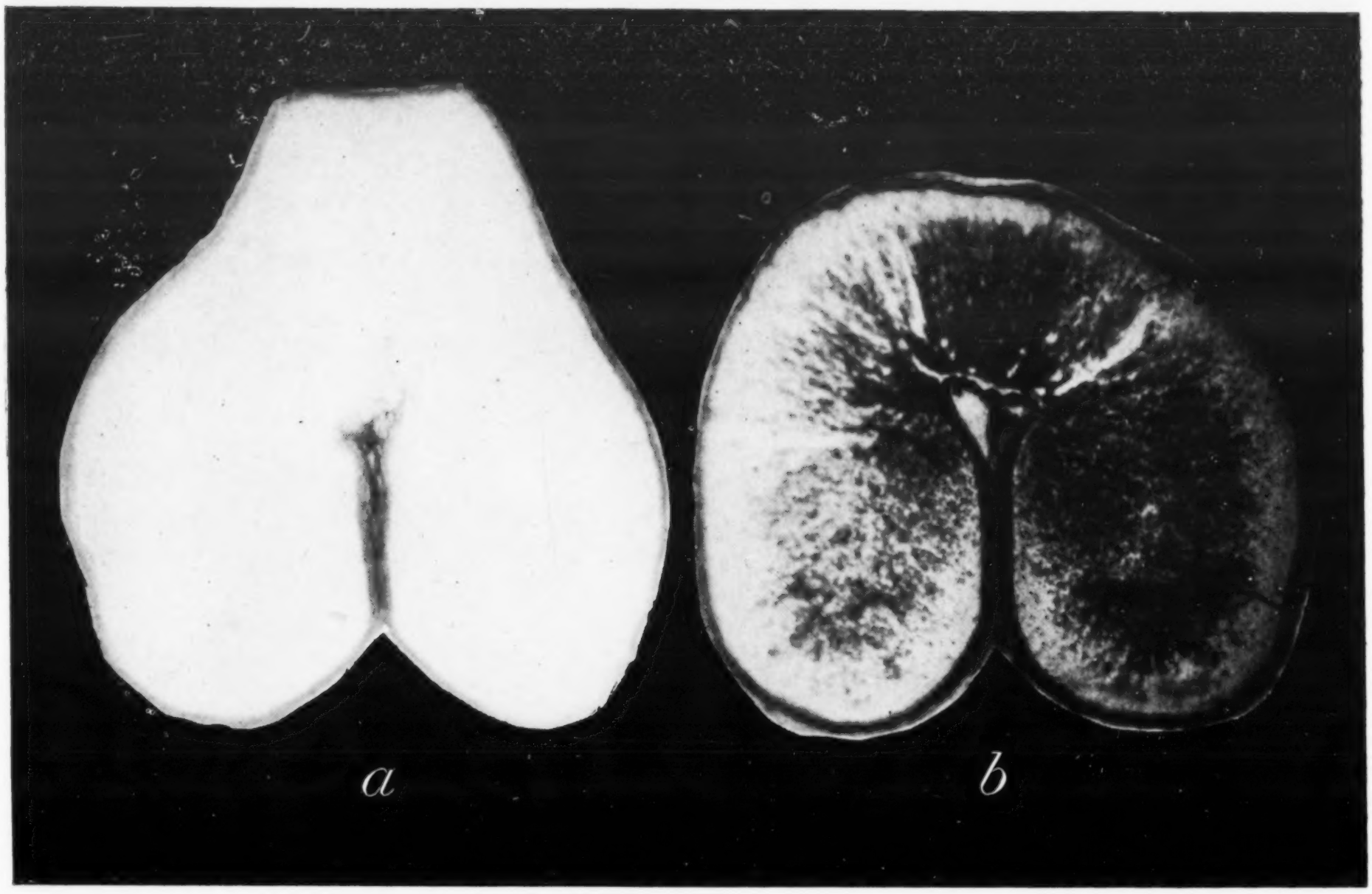
ECONOMIC wheat breeding always has for its aim the improvement of either the yield or the quality of grain or perhaps both. These objects are sought through many contributing sub-characters such as drought or disease resistance, stiffness of straw, time of maturity, texture of grain, size of berry, chemical composition, etc. As a character indicative of quality, the texture of the grain is usually considered important. A soft opaque texture is generally recognized as being associated with a low protein content whereas a horny translucent grain is characteristic of highly glutinous wheats. While quality, as well as quantity, of gluten ultimately determines the milling and baking value of a wheat, high gluten content is usually associated with the production of the best grades of flour. Whereas the writer has shown[1] that there are varieties of bread wheats which will maintain their hard horny texture in a warm irrigated district, the low yield of these strains when compared with the softer sorts, soon results in the elimination of the former group in any mixture where both are present, as is the case with practically all commercial planting. The result is that so nearly all of the wheat produced in warm, humid regions is soft in texture and of low gluten content that the public have come to believe that only soft wheat of inferior grade can be grown in such a region. Wheat breeders in such countries are, therefore, concerned with the production of varieties which are able to resist this softening tendency of the warm climate, and which are, at the same time, good yielders. It has also been shown (1. c.), that certain varieties of macaroni wheats remain hard when grown by irrigation in southern Arizona, and that, among these, those strains which maintained their hardness were the best yielders. Moreover, when these high yielding macaroni wheats were compared with the best producers among the soft bread wheats, they were found to be fully their equal. Macaroni wheats are not popular for bread making purposes on account of the fact that the loaf is not so large or light as that made from the bread wheats.

Now it was conceived some years ago that the bread-making quality of the high yielding soft wheats might be introduced into the gluten of the equally high yielding hard macaroni wheats, and result in the production of a high grade milling wheat for warm climates.

GOOD MILLING WHEAT FOR WARM CLIMATES

Accordingly, in 1913, reciprocal crosses were made between a white macaroni wheat (No. 1) coming originally from Algeria, a soft red bread wheat (No. 3) also imported from Algeria, and Sonora (No. 35), a soft white wheat commonly grown locally. The present paper gives the results of a study of the inheritance of grain texture through four generations of

[1] Freeman, Geo. F., 1917. A mechanical explanation of the progressive change of proportion of hard and soft wheat kernels. *Journ. Amer. Soc. Agron.*, Vol. x, No. 1 (1918), p. 23.



GREATLY ENLARGED CROSS SECTIONS OF MACARONI AND SOFT WHEATS

Cross sections of wheat grains photographed by transmitted light. (*a*) Pure macaroni. Endosperm texture flinty and translucent. Consequently photographing white. (*b*) Pure Sonora. Endosperm texture soft, rendered nearly opaque by many small diffusely scattered air spaces, which photograph dark. (Fig. 12.)

those crosses in which the macaroni wheat furnished one of the parents.

The difference between the texture of the hard, translucent grains of macaroni wheats and the opaque grains of soft wheats lies in the proportion of gluten to starch and the behavior of these compounds in the ripening of the grain. When sufficient gluten is present the entire cell contents, including the starch grains, remain cemented together, as the grain dries out in ripening, and the decrease in weight occasioned by the loss of water is accompanied by a corresponding shrinkage in the size of the grain. The solidly cemented mass therefore becomes translucent and glassy in texture as the grain approaches the air dry condition. On the other hand, when insufficient gluten is present, the starch grains are not held firmly together and when the grain dries out, instead of shrinking to fully compensate for the loss of water, air spaces appear. These air spaces serve as refracting surfaces and render the grain opaque.

In order to make a microscopical study of grain texture, it is necessary to obtain thin sections without disturbing the physical structure of the grain. The brittleness of hard wheats and the friability of those which are soft make it impracticable to cut thin sections with a razor from the dry grain. On the other hand, if the seed be soaked up with water or other softening solutions the physical structure of the endosperm is disturbed and does not return completely to its former condition when subsequently desiccated. Fortunately these difficulties may be overcome by making sections after the method used by petrologists in preparing thin sections of mineral or fossils for microscopical study. A section about 2 mm. thick is easily cut, or rather broken out, with a knife. By rubbing this section over the surface of a fine, flat file it may be quickly ground down to the thickness of ordinary writing paper. It is then transferred to the clean, dry surface of a yellow Belgian hone upon which it is further polished on both sides. This

polishing may be continued until the section has reached the desired thinness. In these operations the section is held between the ball of the finger and the grinding surface, light pressure being exerted as the section is moved to and fro. A thin, smooth cloth may be used to protect the finger from abrasion. By this means sections of only a few cells thickness and sufficiently transparent for microscopical study, may be prepared without, in any way, disturbing the physical structure of the endosperm. Such sections are best mounted for study directly in balsam, cedar oil, or concentrated glycerine. When viewed by transmitted light the horny solid parts of the endosperm are clear and transparent, and any air spaces present are made prominent as dark objects by the interception of the light. On the other hand, when viewed by reflected light, the air spaces appear as white masses on a dark background.

APPEARANCE OF GRAINS VARIES

The comparative appearance of typical sections of a hard and a soft wheat viewed with transmitted light is shown in Fig. 14. In this plate *a* is from a grain of Algerian macaroni wheat, and *b* is from the Sonora. It should be noted that air spaces are almost entirely absent from the endosperm of the macaroni wheat, and are very abundant and diffuse in the Sonora. The crossed seeds were very much wrinkled and exhibited an endosperm character intermediate between the parents. The seeds of the F_1 plants (F_2 endosperm) were also all wrinkled and more or less intermediate between the parents. There was, however, some variation in texture such as may be shown in the series given in Fig. 15. As is apparent from the plate, the members of this series grade insensibly into one another so that, whereas one may easily distinguish the extremes, the separation of the seeds into hard, intermediate and soft groups would be largely arbitrary. Nevertheless such a separation was attempted in the case of two F_1 plants, and the seeds planted to test the genetic significance of the separation. The results of this test, together with a summary showing the segregation of grain texture in all of the F_2 plants arising from the two macaroni bread wheat crosses here described, are shown in Table I.

TABLE I.—*Segregation of Grain Texture in the Seeds Borne on the F_1 and F_2 Plants of Macaroni Bread Wheat Crosses*

	Hard (*a*)	Intermediate (*b*) and soft (*c*)	
(1 x 35 cross F_1 plant No. 16–1)	23%	77%	
(1 x 35 cross F_1 plant No. 16–5)	14%	86%	
	F_2 plants with seeds		
	All hard (*a*)	Mixtures of hard (*a*) intermediate (*b*) and soft (*c*)	All soft (*c*)
Selected hard[1] seed from 16–1 gave as offspring	12	12	1
Selected soft [3] seed from 16–1 gave as offspring	.....	14	3
Selected hard[1] seed from 16–5 gave as offspring	7	7	1
Selected soft[3] seed from 16–5 gave as offspring	4	13	5
Unselected seed from 16–1 gave as offspring	11	36	17
Unselected seed from 16–5 gave as offspring	19	39	10
Total of 1 x 35 cross gave as offspring	682	1251	336
Percentage in each class	30%	55%	15%
Total of 1 x 3 cross gave as offspring	111	227	30
Percentage in each class	30%	61%	9%

[1] Seeds like Plate II, Fig. *a*. [2] Seeds like P'ate II, Fig. *b*. [3] Seeds like Plate II, Fig. *c*.

These results indicate clearly that the differences observed in the seeds borne on the F_1 plants were genetically significant, but that by mere inspection the separation of the different classes could not be made with complete accuracy. This was, in some measure, due to the wrinkled nature of the seed borne on the F_1 plants. Since many of the F_2 plants bore seeds which were plump, but which still exhibited the hard, intermediate or soft endosperm, separations could be made with much greater but still not complete precision. This is shown in the results of a continuation of the study of the offspring of the F_1 plant No. 16-5 into the third generation. An F_2 plant of the 1915 crop (No. 16-5-1-15) having seeds recorded as 28% hard (*a*) and 72% intermediate (*b*) or soft (*c*) was planted indiscriminately (as No. 263) and gave, in 1916, 49 plants of which 8 (16%) had all hard (*a*) seed; 32 (65%) had a mixture of hard (*a*) intermediate (*b*) and soft (*c*) seeds and 9 (19%) had all soft seed (*c*). Selected seed from the same mother plant gave the following results:

TABLE II.—*Inheritance of Endosperm Texture in Macaroni Bread Wheat Crosses*

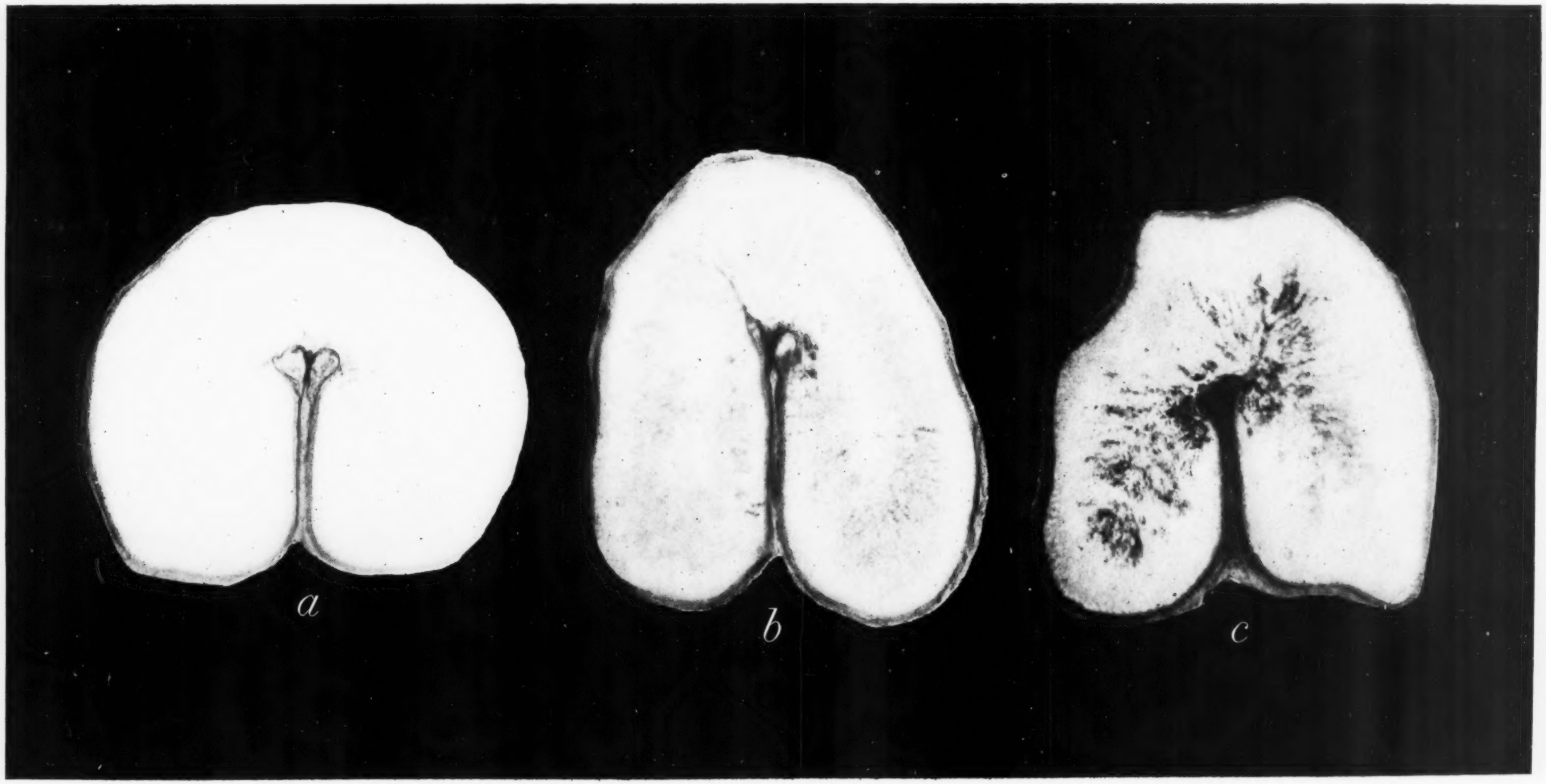
	F_3 plants with seeds		
	All hard (*a*)	Mixtures of hard (*a*) intermediate (*b*) and soft (*c*)	All soft (*c*)
Selected hard (*a*) seed of No. 16–5–1–15 gave as offspring	39	8	
Selected soft (*c*) seed of No. 16–5–1–15 gave as offspring	.....	27	17

(*a*) Like Plate III, Fig. *a*. (*b*) Like Plate III, Fig. *b*. (*c*) Like Plate III, Fig. *c*.

Six plants from the offspring of No. 263 were selected for a further study. The nature of the seeds borne on these selected plants and the character of their offspring are summarized in the following table:

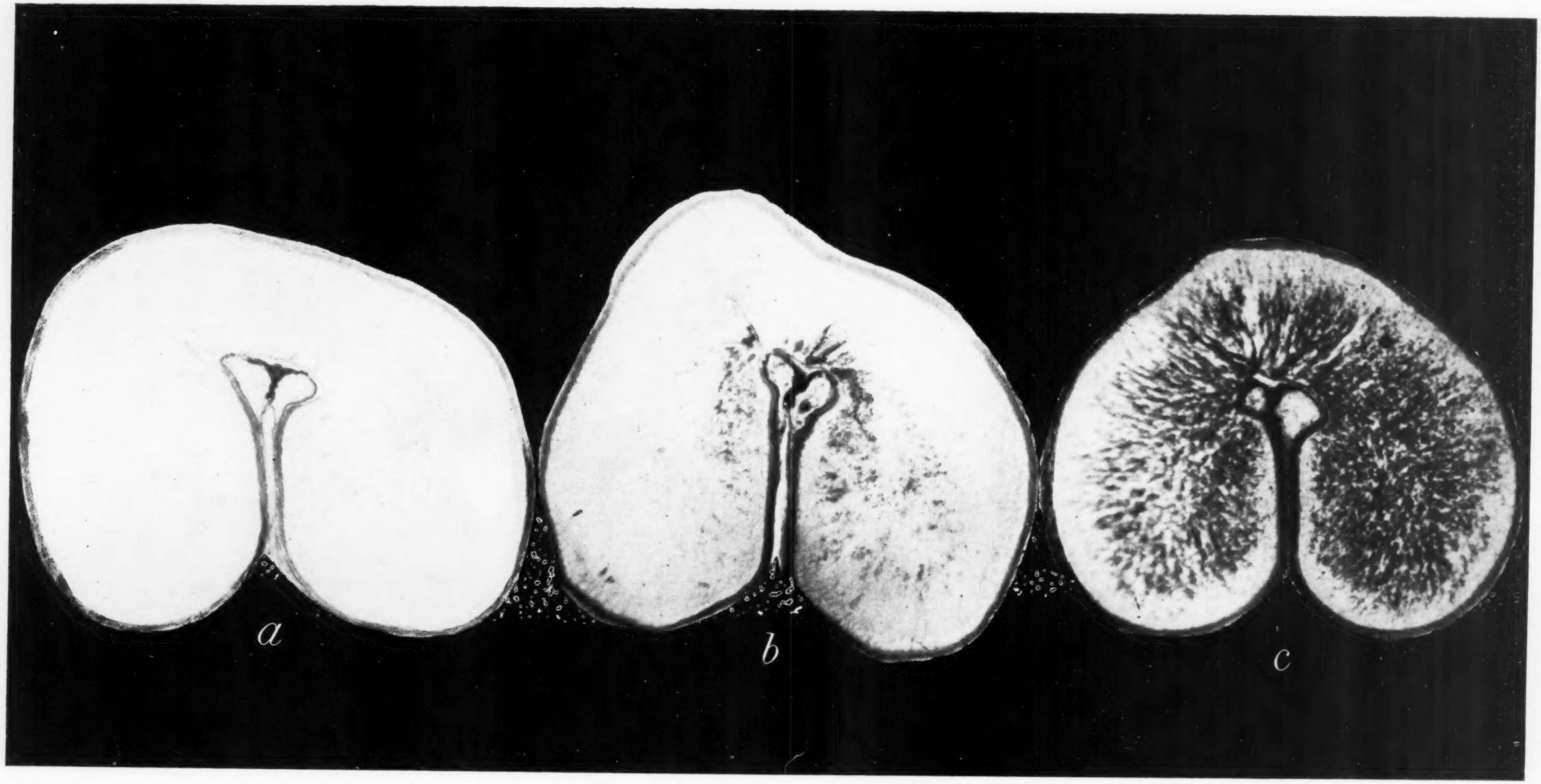
TABLE III.—*Inheritance of Endosperm Texture in Macaroni Bread Wheat Crosses*

Selected mother plant No.	Character of seed of mother plant			Kind of seed selected for planting	Character of offspring in 1917					
					F_4 plants having seeds					
	Hard (*a*)	Intermediate (*b*) or soft (*c*)	Soft (*c*)		All hard (*a*)		Mixture of hard (*a*) intermediate (*b*) and soft (*c*)		All soft (*c*)	
	Per cent	*Per cent*	*Per cent*		*No.*	*Per cent*	*No.*	*Per cent*	*No.*	*Per cent*
263–7	.....	.....	100	Soft (*c*)	.....	.....	.....	.....	45	100
263–14	52	48	.....	Hard (*a*)	22	49	23	51	.....	.....
				Soft (*c*)	.....	.....	9	20	36	80
263–23	100	.....	.....	Hard (*a*)	45	100	.....	.....	.....	.....
263–30	66	34	.....	Hard (*a*)	28	61	18	39	.....	.....
				Soft (*c*)	.....	.....	18	45	22	55
263–48	100	.....	.....	Hard (*a*)	35	100	.....	.....	.....	.....
263–49	.....	.....	100	Soft (*c*)	.....	.....	.....	.....	47	100



ENLARGED CROSS SECTIONS OF FIRST GENERATION WHEAT HYBRID KERNELS

Cross sections of seeds from an F_1 plant of a macaroni-Sonora cross. Air spaces of the diffuse type. (*a*) When planted gave predominantly hard seeded plants. (*b*) When planted gave predominantly soft seeded plants. See Table I. (Fig. 13.)



ENLARGED CROSS SECTIONS OF SECOND GENERATION WHEAT HYBRID KERNELS

Cross sections of seed from an F_2 plant of a macaroni-Sonora cross, which was heterozygous for grain texture Opaqueness variable in amount, but all of the diffuse type. (*a*) when planted gave seeds predominantly hard; (*b*) when planted gave a mixture of all types; (*c*) when planted gave seeds predominantly soft. See Tables II and III. (Fig. 14.)

It will be noted from this table that whenever the parent plant had grains all soft or all hard, the parental character was followed in all of the offspring. When, however, the parental plant exhibited its hybrid nature by a mixture of grain types, the offspring varied according to the type of seed planted. Selected hard seed produced either plants having all hard seed or else plants having a mixture of hard and intermediate seeds, but no plants having soft seeds. Again, selected soft seed produced plants having a mixture of intermediate and soft seed or else plants with all soft seeds, but no plants having hard seeds. We may assume that seeds giving rise to plants having a mixture of grain types are heterozygous with regard to endosperm texture, whereas those giving rise to plants having seeds either all hard or all soft are homozygous with regard to these characters. The above results indicate therefore that we are unable, accurately to distinguish between hard and intermediate (homozygous and hybrid hard) grains, on the one hand, and between intermediate and soft (hybrid and homozygous soft, grains, on the other hand, but we mistake a homozygous hard grain for a homozygous soft one.

In the summer of 1915 a large number of plant selections were made from the F_2 plants of the macaroni bread wheat crosses from which plant rows were sown in the fall of the same year. A study of the inheritance of grain texture in the resulting F_3 generation harvested in the spring of 1916 can be summarized in the following table:

TABLE IV.—*Inheritance of Grain Texture in the F_3*, 1916

Character of seeds on the F_2 selected mother plants	Number of such mother plants selected	Character of seeds on F_3 offspring: No. plants having seeds		
		All hard (*a*)	Mixture of hard (*a*) intermediate (*b*) and soft (*c*)	All soft (*c*)
1 x 35 Cross				
All hard (*a*)	65	2,798		
Mixture of hard (*a*), intermediate (*b*) and soft (*c*) grains	23	694	114	
	7	145	107	
	25	154	668	163
	2	.....	57	
	20	.....	574	249
All soft (*c*)	59	.....	755	1,715
	9	.....	.....	412
1 x 3 Cross				
All hard (*a*)	21	913		
Mixture of hard (*a*) intermediate (*b*) and soft (*c*) grains	2	50	27	
	33	33	253	77
	12	.....	276	226
All soft (*c*)	6	.....	68	108
	4	.....	.....	188

(*a*) Like Plate III *a*
(*b*) Like Plate III *b*.
(*c*) Like Plate III *c*.

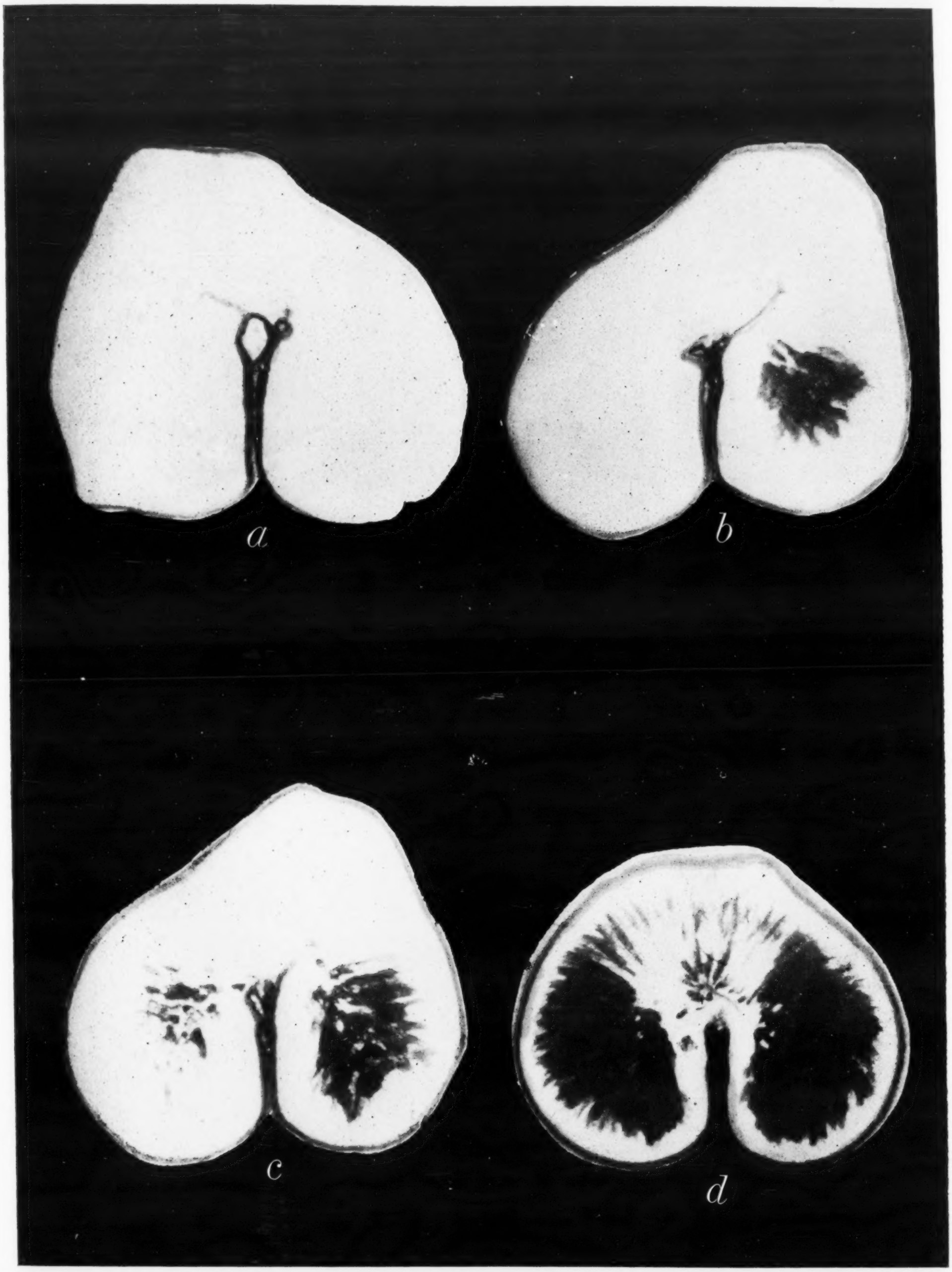
The results shown in Table IV coincide fully with those exhibited by Table III. It should be remarked that in all of the above tables the group headed "mixture of hard, intermediate, and soft," contains at least three types of plants, as follows: (1) Those bearing a mixture of hard and intermediate grains; (2) those with a mixture of hard, intermediate and soft grains, and (3) those with a mixture of intermediate and soft grains. These types so insensibly grade into one another that it was found impracticable to separate them. It may, however, be stated that where the offspring of a given mother plant segregate only into plants with all hard seed, and those with a mixture of types and none with all soft seed, the seeds on those plants with mixed types tend toward the harder limits of the series, *i. e.*, they fall into type (1) of the series described above. When the offspring of a single mother plant segregate into plants having all hard seeds, plants with a mixture of types and plants having all soft seeds, then many of the plants having seeds of mixed types show every gradation of seed type from hard through intermediate to soft. Again, when the offspring of a single mother plant segregate into plants having a mixture of seed types and plants with all soft seeds, the seeds on the plants having a mixture of types tend strongly to fall into the softer end of the series, *i. e.*, to consist of a mixture of intermediate and soft seeds. The character of the seed on mother plants having a mixture of seed types gives a strong indication of the kind of segregation to be expected in the offspring. If they fall within the harder end of the series they tend to give only plants with all hard seeds, and plants with a mixture of hard and intermediate seeds. If they lie nearer the softer end of the series, then the offspring tend to segregate only into plants having a mixture of intermediate and soft seed and plants with all soft seeds. Finally, if the mother plant contains all types of seed, then all types of plants may be expected among the offspring. The continuous intergradation of seed types would render any numerical separation purely arbitrary. A judgment of the genetic composition of the parent by the behavior of its offspring is, therefore, here, as in many other cases, the only sure means of analysis.

TWO FACTORS APPEAR PRESENT

A genetic analysis of the data presented can be made by assuming that the relative proportion of gluten and starch in the endosperm of the wheat varieties studied is controlled by two factors, the intensity of the action of which may be varied within somewhat narrow limits by environic conditions in the same manner that the intensity of action of other factors governing quantitative characters are varied by their environment. The combination of these variations, partly genetic and partly environic, are, therefore, amply sufficient to account for the intergradation of grain types and the impossibility of making exact numerical separations.

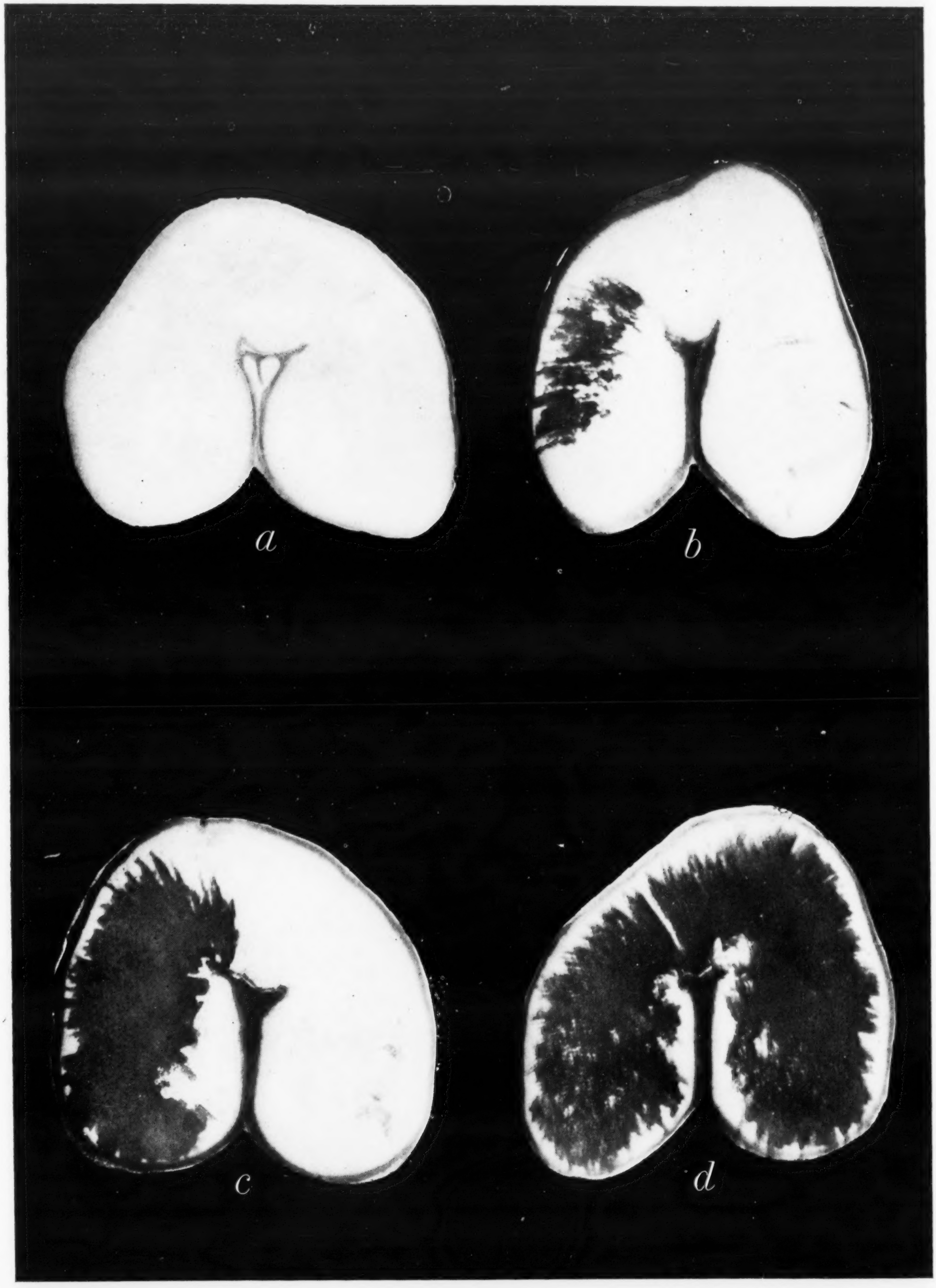
With these ideas in view, let us now assume two factors for increasing the percentage of tarch A and B having incomplete dominance over their absence and being accumulative in their action. Let us suppose further that (by the standards of comparison used by the writer) the presence of three A's together with at least one B in the endosperm cells (assuming double fertilization) of a grain were sufficient to cause it to be classed as soft, whereas less than three A's and B's counted together would result in an endosperm which would be graded as "hard." All other seeds would be graded as "intermediate."

The genetic composition of the F_2 embryos, and, hence, of the somatic tissue of the F_2 plants arising therefrom, together with the genetic structure of the endosperm of the seeds and embryos borne on these plants, can be placed in tabular form as follows:



MACARONI WHEAT KERNEL CROSS SECTIONS SHOWING YELLOW BERRY SPOTS

Cross sections of the seed of a pure macaroni wheat plant, showing a clear hard grain (*a*) and varying sizes of yellow-berry spots (*b*, *c*, *d*). The air spaces causing these opaque spots, lie in plates with quite definite margins. The proportion of gluten to starch is roughly indicated by the light and dark areas. (Fig. 15.)



HYBRID WHEAT KERNEL CROSS SECTIONS SHOWING YELLOW BERRY SPOTS

Cross sections, greatly enlarged, of the seed from an F_2 plant of a macaroni-Sonora cross which was homozygous for hard grains but which showed a small percentage of grains with yellow-berry spots. When planted, all of these types gave practically the same results. The dark areas are proportionately richer in starch than the light ones. See Table IX. (Fig. 16.)

TABLE V.—*Factorial Analysis of the Heredity of Grain Texture*

					Comparison of theoretical with found results in F_2		Comparison of theoretical with found results in the F_3		
Genetic formulae of F_2	Genetic formulae of F_2 embryos	Genetic formulae of F_2 endosperm borne on F_2 plants	Grade of individual seed	Grade of seed of plant as a whole recorded in table	Percentage of plant expected in this group	Percentage of total No. of plants found in this group. (Summary of both crosses in Table I)	Type of grain	Percentage of total No. of plants expected of each type	Percentage of F_3 plants found in each type. (Summary of both F_3 crosses in Table IV)
ABAB	ABAB	ABABAB	Soft				Soft	100	100
ABAb	ABAB	ABABAB	Soft		19	14	Soft		
	ABAb	ABABAb	Soft	Soft			Inter-	75	69
	AbAB	AbAbAB	Soft				mediate	25	31
AbAB	AbAb	AbAbAb	Inter-mediate						
ABaB	ABAB	ABABAB	Soft				Soft	25	35
	ABaB	ABABaB	Inter-mediate				Inter-	75	65
	aBAB	aBaBAB	Inter-mediate				mediate		
aBAB	aBaB	aBaBaB	Inter-mediate						
	ABAB	ABABAB	Soft						
ABab	ABAb	ABABAb	Soft						
	AbAB	AbAbAB	Soft						
	AbAb	AbAbAb	Inter-mediate						
	ABaB	ABABaB	Inter-mediate				Soft	19	18
abAB	aBAB	aBaBAB	Inter-mediate				Interme-diate or mixed	50	68
	ABab	ABABab	Inter-mediate	Inter-mediate or mixed	50	56	Hard	31	14
	abAB	ababAB	Hard						
	AbaB	AbAbaB	Inter-mediate						
AbaB	aBAb	aBaBAb	Inter-mediate						
	Abab	AbAbab	Hard						
	abAb	ababAb	Hard						
	aBaB	aBaBaB	Inter-mediate						
aBAb	aBab	aBaBab	Hard						
	abaB	ababaB	Hard						
	abab	ababab	Hard						
AbAb	AbAb	AbAbAb	Inter-mediate						
aBaB	aBaB	aBaBaB	Inter-mediate				Inter-mediate	100	100
	AbAb	AbAbAb	Inter-mediate						
Abab	Abab	AbAbab	Hard						
	abAb	ababAb	Hard						
abAb	abab	ababab	Hard				Inter-mediate	25	22
	aBaB	aBaBaB	Inter-mediate				Hard	75	78
aBab	aBab	aBaBab	Hard	Hard	31	30			
	abaB	ababaB	Hard						
abaB	abab	ababab	Hard						
abab	abab	ababab	Hard				Hard	100%	100%

In view of the almost perfect intergradation of types as already explained and, hence, the difficulty of making exact numerical separations, the data actually found and the theoretical expectations show a rather remarkable closeness of fit. Especially noteworthy is the fact that all of the theoretically expected groups are present, and in no case behave in a manner contradictory to the assumed factorial explanation.

Many students of grain texture in wheat have been confused and misled by the occurrence of so-called "yellow berry" in hard wheats. Many wheats which in a northern or dry climate produce hard, translucent grains, in a more humid or southern climate will produce a greater or less proportion of grains containing opaque spots in the endosperm. Grains containing such spots are commonly called "yellow berries." When the opaque spot is extended to include all or nearly all of the endosperm, the whole grain appears to be opaque and may be easily mistaken for an ordinary soft wheat. The difference, however, is, in most cases, easily determined by a microscopic examination of thin sections prepared as described above. Fig. 16 gives several types showing the intergrading series from a true hard to a true soft wheat, indicating that grain texture is a quantitative character depending, in all probability, upon the relative proportions of starch and gluten in the endosperm as previously explained. These were all from the seeds of a single hybrid wheat plant which was heterozygous for grain texture. Fig. 17 gives a paralllel series from a single plant of a pure race of a hard wheat (Algerian macaroni), and exhibits several types extending from a grain which was translucent throughout, to those with larger and larger "yellow berry" spots until the endosperm of the seed at the right is practically all included in the yellow spot. Fig. 18 gives a similar series taken from an F_2 macaroni Sonora hybrid plant which was homozygous for hard grain texture. Comparing Fig. 16 with Figs. 17 and 18 one readily sees that the air spaces causing the opaqueness of the "Yellow Berry Spot" lie in flakes, whereas those of the true soft wheat are diffuse.

HEREDITY OF "YELLOW BERRY"

The heredity of the diffuse or true softness has been shown and discussed above. We may now investigate the nature and heredity of "Yellow berry." The following table gives a number of selected cases showing the variation in the percentage of yellow berry in pure lines of hard wheats in different years and when grown under different environic conditions in the same year:

TABLE VI.—*Environic Variations in Percentage of "Yellow Berry" Grains in Pure Lines of Hard Wheat*

Pedigree No.	Environic condition	Percentage of yellow berries in crop of		
		1914	1915	1916
36–19	Nursery row Yuma	35	10	0
36–20	Nursery row Yuma	97	54	7
36–21	Nursery row Yuma	31	43	0
36–43	Nursery row Yuma	36	50	2
36–43	Increase plot Yuma	.....	95	35
36–51	Nursery row Yuma	15	28	0
36–51	Increase plot Yuma	.....	96	42
36–81	Nursery row Yuma	11	33	4
36–81	Increase plot Yuma	.....	85	35
3–12	Nursery row Yuma	0	96	12

Where the percentage of yellow berries was large, the opaque spots were large and frequently included the entire endosperm. On the other hand, where the percentage of yellow berries was small, the opaque spots were small

and there was but few cases where they included more than half the endosperm.

An F_2 plant (No. 16-1-2-13) of the 1915 crop, having hard seeds (20% translucent throughout, 80% with opaque spots, *i. e.*, "yellow berries") was chosen, and 50 unselected seeds planted as No. 239. In the spring of 1916, these gave 34 plants all having seeds classed as hard, but among which there were an average of 23% of "yellow berries." The distribution of the percentages of yellow berry among these plants may be given as follows:

TABLE VII

Per cent yellow berry.	0	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100
No. plants.....	8	8	6	3	2	1	1	2	1	1	1

Going back to the original plant (No. 16-1-2-13), 25 translucent and 50 yellow berry seeds were selected and planted in adjoining nursery rows with the following results:

TABLE VIII

Per cent yellow berry	0	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	Total No. plants	Average per cent yellow berry
Plants from translucent seeds.....	14	....	1	.....	.....	1	.....	.....	1	.....	.....	17	8
Plants from yellow berry seeds.....	18	9	1	3	2	3	.....	.....	1	.....	1	38	12

In the fall of 1916 seeds from five plant selections from No. 239 were planted. The nature of the seed planted and the crop obtained are summarized in the following table:

TABLE IX.—*Heredity of Yellow Berry*

Parental No.	Per cent yellow berry in mother plant	Pedigree No.	Kind of seed selected	Distribution of percentages of yellow berry in plants of offspring					Total No. plants	Average per cent of yellow berry
				0	1–10	11–20	21–30	31–40		
239–7	87	1006	(*c.*, *d.*) Yellow berry (*a*)	18	15	4	1	1	39	4
239–7	87	1005	Translucent (*c.*, *d.*)	19	4	1	.....	.....	24	1
239–18	57	1010	Yellow berry (*a*)	15	12	3	1	2	33	5
239–18	57	1009	Translucent (*c.*, *d.*)	24	17	.....	1	1	43	2
239–33	29	1012	Yellow berry (*a*)	31	12	.....	1	.....	44	1
239–33	29	1011	Translucent (*c.*, *d.*)	31	11	1	1	.....	44	2
239–10	100	1007	Yellow berry (*a*)	20	14	5	3	1	43	5
239–19	0	1008	Translucent	33	2	.....	.....	.....	35	0

(*a*) Like Fig. 18 (a). (*c*) Like Fig. 18 (c). (*b*) Like Fig. 18 (b). (*d*) Like Fig. 18 (d).

While one may see in this table a slight tendency of the yellow berry seed to produce a higher percentage of yellow berry in the offspring, the differences are so slight and the regression so strong that one may easily question its significance. A comparison of Tables III and IX is sufficient to convince one immediately that the heredity of yellow berry is at least something wholly different from that of true hardness and softness as exhibited in Table III. The study of the diffuse type of opaqueness (softness) has clearly shown that this character (though quantitative and, hence, difficult of exact separation into genetic classes) is strictly hereditary. It may, moreover, be pointed out that pure lines of true soft wheats (diffuse type) such as Sonora, Algerian Red Bread, and Early Baart are 100% opaque[2] every year, and never exhibit environic variations in hardness such as is shown by pure lines of hard wheats, examples of which are given in Table VI.

DEPENDENCE ON ENVIRONMENT

The great dependence of yellow berry on environic conditions and its almost complete regression from the selection of extreme variants, suggest strongly that this is quite largely a physiological response. True, a tendency toward greater or less sensitivity of this response may be inherited and it may be possible that those grains in a head carrying genetic factors for greater sensitivity would be the first to respond to environic conditions tending to favor the yellow berry character whereas those same grains under conditions favoring greater hardness would have remained perfectly translucent throughout. This would account for the slight but quite uniform differences exhibited in tables VIII and IX. Convincing proof that the tenddency toward the production of yellow berry in hard wheats is hereditary is shown in an experiment with 145 pure races of turkey wheat extending through the years 1914, 1915 and 1916. Here the correlation of the percentage of yellow berry in 1914 with the same in 1915 was $+57\% \pm 4\%$, whereas that between 1915 and 1916 was $+33\% \pm 5\%$, and between 1914 and 1916 was $+41\% \pm 5\%$. These correlations being more than six times their probable errors are certainly significant.

Among the F_2 plants originating from the Macaroni-Sonora cross, there were 65 which had grains recorded as all hard (or with a greater or less percentage of yellow berry), and which gave all hard or "yellow berry" offspring, *i. e.*, produced no plants having any intermediate or soft grains (diffuse type).[3] Many of these, however, contained a greater or less percentage of "yellow berries." The correlation calculated between the percentage of yellow berries in these parents and the average percentage of yellow berries in their offspring was $+51\% \pm 6\%$.

REGRESSION IN PARENTAL STRAINS

The strong regression from extreme selections, but still quite definite inheritance of the tendency to produce yellow berry, is perhaps better shown by arranging the parental strains or mother plants in accordance with the percentage of yellow berry they contain and then showing the distribution and average of their respective offspring as is done in the Table X.

The arrangement here shown was made so as to divide the parental strains or plants, as nearly as possible, into three equal groups. While the differences between the groups are not large, the numbers involved and the uniformity of results certainly render them significant.

CONCLUSIONS

1. The hardness of a wheat is determined by the solidity of the grain, and this, in turn, by the nature and relative proportions of gluten and starch in the endosperm.

2. When the ratio of gluten to starch

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[2] Like Plate I, Fig. *b*.
[3] Like Plate III, Figs. *b* and *c*.

TABLE X.—*Inheritance of Percentage of Yellow Berry in Hard Wheats*

Percentage of yellow berry in parents	Average percentages of yellow berry in offspring																				No. of races	Average percentage of yellow berry
	0	1–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–36	37–40	41–44	45–48	49–52	53–56	57–60	61–64	65–68	69–72			
145 pure races of Turkey wheat; crop of 1914 compared with that of 1915																						
0–24	1	8	8	6	7	1	4	3	2	3	3	1	4	1	...	...	1	...	...		53	20
25–49	1	3	5	2	3	4	4	3	1	2	3	5	2	3	...	2	2	1	...		46	29
50–100	...	...	1	1	2	2	5	6	5	4	7	5	1	...	4	...	2	...	1		46	34
145 pure races of Turkey wheat; crop of 1914 compared with that of 1916																						
0–24	38	11	3	1	...																53	1
25–49	26	13	1	4	...		1	...	1	...											46	3
50–100	19	15	6	4	...			1	...	1	...										46	4
145 pure races of Turkey wheat; crop of 1915 compared with that of 1916																						
0–19	36	14	1	3	...																54	1
20–39	27	15	4	4	...																50	2
40–100	20	10	5	1	...	1	1	...	1	1	...										40	5
65 homozygous hard wheats of hybrid origin (Macaroni-Sonora)																						
0	9	14	3	2	1	...	...	1	...												30	4
1–13	5	4	4	...	2	...	...	...	...												15	5
14–91	...	4	5	4	3	...	2	2	...	...											20	11

is sufficiently high, the entire cell contents are cemented together solidly as the grain dries out in ripening. It, therefore, takes on a hard, glassy, semi-translucent texture. In the absence of a sufficient proportion of gluten to hold the cell contents together, the shrinkage in drying does not fully compensate for the loss of water, and air spaces appear within the cells. These open spaces render the grain soft and, also, since they serve as refracting surfaces, make it opaque. We are, therefore, accustomed to associate softness, opaqueness and low gluten content in wheats.

3. There are two types of soft grains among the wheats included in these experiments.

(*a*) A type designated by the writer as "true softness" in which the air spaces in the endosperm are diffuse and finely scattered. This type of softness is only slightly affected by environic conditions.

(*b*) A type commonly called "yellow berry" in which the air spaces within the endosperm occur in flake-like groups with quite definite margins. The opaqueness thus arising may be confined to a small spot only or may include the entire endosperm. This type of softness is very sensitive to environic conditions.

4. The genetic behavior of "true softness" in the wheats crossed by the writer may be explained by two independent factors governing the relative proportion of gluten and starch. These factors show incomplete dominance over their absence, and appear to be accumulative in their action, *i. e.*, the intensity of their action depends upon the number of times the factors appear in the endosperm. Thus (assuming double fertilization) the presence of none to six factors in the endosperm cells gives rise to a series of types grading from hard (translucent) through almost insensible degrees to completely soft (opaque) grains.

5. The genetic factors governing the appearance of "yellow berry" have not been fully analyzed, but they are evidently distinct from those which give rise to "true softness." These factors are very sensitive to environic influences, and changes in climatic, soil, and cultural conditions so vary the intensity of their action as almost to cause one to overlook their hereditary nature. However, in spite of the strong regression from extreme selections, the almost perfect uniformity of results from a number of carefully controlled experiments indicate that genetic factors, for a greater or less sensitivity, are inherited as definitely as are other factors governing quantitative characters. The number of factors involved have not been determined.

Selection of Laying Hens

Since it is always of prime importance to keep only the best layers in any flock of hens, many tests have been devised for selecting good layers. Some of these, such as the trap-nest, have been technically satisfactory, but have proven too difficult of operation for the average breeder, while many others have been found to contain a minimum of substance as well as a maximum of superstition.

It has been observed that paling of the leg color is often correlated with heavy laying, which is only natural, since a three pound bird, may store away more than her own weight of fatty and nitrogenous substances in the 150 eggs she lays. It has been found[1] that by measuring the amount of yellow pigment in the body fat, the hens may be graded according to their egg records.

The findings of the bulletin may be summarized as follows:

The laying activity causes loss of yellow pigment in the body fat of various breeds of the domestic fowl. A cessation of laying causes a return of the yellow pigment.

The ear lobes, vent and beak are the parts most quickly responsive to a change in laying activity, while the legs are the last to respond. By taking measurements of pigmentation in October, the average past egg record can be estimated. The ear lobes are most readily graded by means of the color top.

When thus graded, the per cent yellow in the ear lobes in October shows a relatively close relationship with annual egg production. (This relationship, expressed mathematically in terms of the correlation coefficient, is between —.5 and —.6.) This relationship is an indirect one, being dependent upon the correlation existing between the laying activity of the period preceding the pigment measurements and the annual egg production.

The changes in body pigment may be used to advantage in separating the high from the low producers. The selection for breeders can best be done in October, when only the high producers are laying.

Other characters besides paling of yellow pigment, viz.: bright color and full size of comb and late molting, may indicate good laying ability. The "Standard of Perfection" in demanding yellow beaks and yellow legs penalizes production. Changes should be made in the score cards in order to insure in poultry shows better as well as more beautiful birds.

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[1] Pigmentation and Other Criteria for the Selection of Laying Hens. Albert F. Blakeslee and J. Arthur Harris, station for Experimental Evolution, Cold Spring Harbor, L. I.; D. E. Warner, Connecticut Agricultural College; Wm. F. Kirkpatrick, Storrs Agricultural Station. Storrs Agricultural Experiment Station, Storrs, Conn. Bulletin 92, December, 1917.

COLOR INHERITANCE IN MAMMALS

XI, Man—Mode of Inheritance of Unusual Family Traits Easy to Analyze. Situation More Obscure in Case of Common Variations. Variations in Hair, Skin, and Eye Color Must be Considered Together. At Least Two Distinct Kinds of Dilution of Color Probably Exist, Which Are Combined in the Blond Nordic Race

$1a_1$	W, w	W—Premature grayness of certain families.
$1a_2$	V, v	V—white spotting.
$1a_3$	——	
1b	C, c	c—albinism in many cases. Variations of this class, common in white race, reduce dark eyes to light, red hair to flaxen, but have little effect on black hair. Reduction of skin color.
$2a_1$	——	
$2a_2$	——	
$2a_3$		Variations of this class, common in white race, reduce dark eyes to light or even albinotic, black hair to red, yellow, flaxen, or white, depending on factors of class 1b. Auburn and brown intermediate variations. Reduction of skin color.
2b	——	

AMONG human beings, the common variations in hair, skin, and eye color resemble many of those of the lower mammals. In spite of this similarity, however, the mode of inheritance is, in most cases, still very obscure. It is only in the case of certain rare variations which are obviously associated with particular families that unit factors can be said to be conclusively demonstrated.

PREMATURE GRAYNESS

A typical example of such a variation is present in a pedigree (MM) given by Pearson, Nettleship, and Usher.[1] Among the affected persons of this family, the hair became gray in youth. In each case, one parent was prematurely gray, while the normal children showed no tendency to transmit the trait. In the published pedigree, the trait has been handed on for at least five generations without a break. Probably it went much farther back as the authors give a translation of an old Gaelic curse said to have been pronounced in the fourteenth century.

"In the time of most numbers shall weakness come o'er them,
In the time of most weakness, shall strength then restore them,
In their prime in their youth like the rushes they'll grow,
As withers the bracken be their manhood laid low,
O'er the child's clustering ringlets shall age spread its snow."

We have here clearly a dominant hereditary unit which is passed on indefinitely without attrition in spite of union with fresh normal stock in each generation. As regards its relationship to color factors in the lower mammals, it seems closest to those which have been put in class $1a_1$. There is a general inhibition of hair pigment regardless of quality. The dominant factor for grayness in horses has the further similarity in that the whiteness increases with age.

Holmes and Schofield[2] have recently published a pedigree in which a small white lock was present only in males, but could be transmitted by the mother. The inheritance was not sex-linked, as affected males could transmit it to their sons. The authors attribute it to sex-limited inheritance. According to this view, the trait is inherited as a dominant unit by the usual mechanism, but

[1]Pearson, K., E. Nettleship, and C. H. Usher, 1913, "A Monograph on Albinism in Man." Dulau and Co., London.

[2]Holmes, S. J., and R. O. Schofield, Jour. Her., 1917, 8:359-362.

is either unable to manifest itself at all in females or else does so only when homozygous as in the case of horns in sheep or the mahogany color in Ayrshire cattle.

The spot is not present in childhood, but develops at puberty. The authors think it probable that hormones developing at that time may be essential. They note that in one of the pedigrees given by Pearson, Nettleship, and Usher, a small occipital spot was inherited in a similar manner.

WHITE SPOTTING

Another peculiar color character, the heredity of which is easily traced, is the piebald or white spotted condition. In piebald individuals the skin is wholly devoid of pigment in irregular areas especially on the ventral surface of the body, on the face and on the head. There is much variation in the amount of white spotting. In some families there is only a white flare in hair above the forehead or a small, white spot on the head. Such a variation is naturally most conspicuous in the colored races, and spotted negroes have often been exhibited at shows. Simpson[3] and Castle studied such a case, and found the piebald condition to be inherited for at least three generations without a break. The trait clearly followed the mechanism of a unit dominant factor. Pearson, Nettleship and Usher[4] have collected together a number of pedigrees involving piebalds. Some of these extend for six generations, but in all cases, with the exception of the sex-limited spot already noted, the trait is transmitted as a dominant unit.

An interesting family history in which a white flare has been transmitted for at least six generations, and probably more, was published by Miller.[5] Here, as in the case of premature grayness cited above, we find the old family tradition, so commonly found where a peculiar trait behaves as a dominant unit. In this case the white spot is said to have originated in a posthumous son of Harry "Hotspur" Percy, born in 1403. Its appearance was attributed to an action of Lady Percy in pressing her hands to her forehead when she swooned on hearing of her husband's death at the battle of Shrewsbury.

Piebald has been spoken of as dominant, but we do not know what a homozygous piebald would be like. As Castle and Simpson pointed out, such an individual might be so nearly unpigmented that the trait would be more nearly recessive than dominant. Such an individual could only come from the union of piebald with piebald. Again, piebald has been spoken of as a unit. This is certainly true in each particular family, but it is not certain that it is the same unit in each case. We might get two factor ratios after a union of piebald with piebald.

ALBINISM

Albinism is a third peculiar color trait the mode of inheritance of which is usually easy to understand. Pearson, Nettleship, and Usher[6] have collected together an enormous amount of information in regard to albinos, including over 600 pedigrees. The trait is found sporadically among all races of the world. There is much variation in the degree. In the most extreme cases there is exceedingly little, if any, pigment in skin, hair, and eyes. The hair is white, the skin white and very easily burned by the sun, and the eyes have a pale gray iris and a red reflection through the pupil in the proper light. There is photophobia, imperfect vision, and nystagmus, all doubtless due to the defective pigmentation of the retina.

Among Europeans, however, no sharp line can be drawn between albinism and extreme blondness. Here the photophobia, imperfect vision, and nystagmus are usually considered the criteria. These may be combined with light brown, pale yellow, or, occasionally, even light red hair, as well as with

[3]Simpson, Q. I., and W. E. Castle, *Amer. Nat.*, 1913, 47:50-56.
[4]Pearson, Nettleship, and Usher, *loc. cit.*
[5]Miller, Newton, JOUR. HER., 1915, 6:165-169.
[6]Pearson, Nettleship, and Usher, *loc. cit.*

the usual white color. The iris is usually pale blue rather than colorless. The skin may show some pigmentation, especially as freckles. In the colored races such freckles are the rule. Even in these races, the gap between normals and albinos is bridged by various dilute types. There are all grades of imperfect albinos which may or may not show visual difficulties.

It is evident that no one unit factor can explain all the phenomena of albinism. Nevertheless, the usual mode of inheritance within families is clear. We do not find long unbroken lines of descent as in premature grayness and white spotting. In a typical pedigree, albinism will be found, perhaps, in several children of a family. The parents may both be normal, but the trait will be found cropping out in several more or less distant cousins. One of the very striking features of pedigrees, as Pearson points out, is the great frequency of cousin marriages among the parents of albinos. Castle[7] and Farabee, as early as 1903, pointed out the probability that albinism behaved as a recessive unit, and Davenport[8] demonstrated it in a considerable number of pedigrees, including three cases in which albino by albino had had only albino children (four in all). Apert[9] analyzed the data of Pearson, Nettleship, and Usher and pointed out that the ratios of albino to normals, correctly interpreted, was close to that expected on the hypothesis of a recessive unit.

The view that albinism is, in general, due to recessive factors may safely be accepted, but it must be pointed out, as in the case of piebalds, that different factors may be involved in different families. The different grades may be due to multiple allelomorphs as found in albino rabbits, guinea-pigs, and rats or may be due to combinations of independent factors or both. It is easy to see that a dilution factor which would produce very little visible effect in the negro race might be enough to reduce a blond European to an albino with imperfect vision and nystagmus. Indeed blondness itself may be looked upon as a grade of imperfect albinism. Another problem is a curious relation of albinism to red hair. Davenport noted that among forty-two parents of albinos in his tables, eleven had some grade of red hair. This is above the usual per cent of red hair in the population involved. About 4% of the population in England, Scotland, or Ireland have distinctly red hair, according to Pearson. The number is larger if we include chestnut, auburn, and yellow. Data collected by Holmes and Loomis[10] at the University of Wisconsin contain 8.8%, including these colors. Pearson noted a similar excess of red among the relatives of albinos in the very extensive data referred to; 13.0% of the parents, 12.9% of the siblings, and 8.6% of the uncles and aunts showed some trace of red. Pearson also emphasizes the point that albinos may have yellow or even light red hair themselves.

These facts seem, at first, very difficult to explain when we recall that in rabbits, guinea-pigs, rats, and dogs, red is very much more quickly reduced to white than is black by grades of imperfect albinism. The subject will be discussed further when the data on the inheritance of red hair are examined. Here it is sufficient to note that albinism cannot always be a single unit. We may say that albinism in most families is due to recessive unit factors, but we must be cautious in identifying the albinism of different families with each other and with the albinism of lower animals.

THE COMMON VARIATIONS IN COLOR

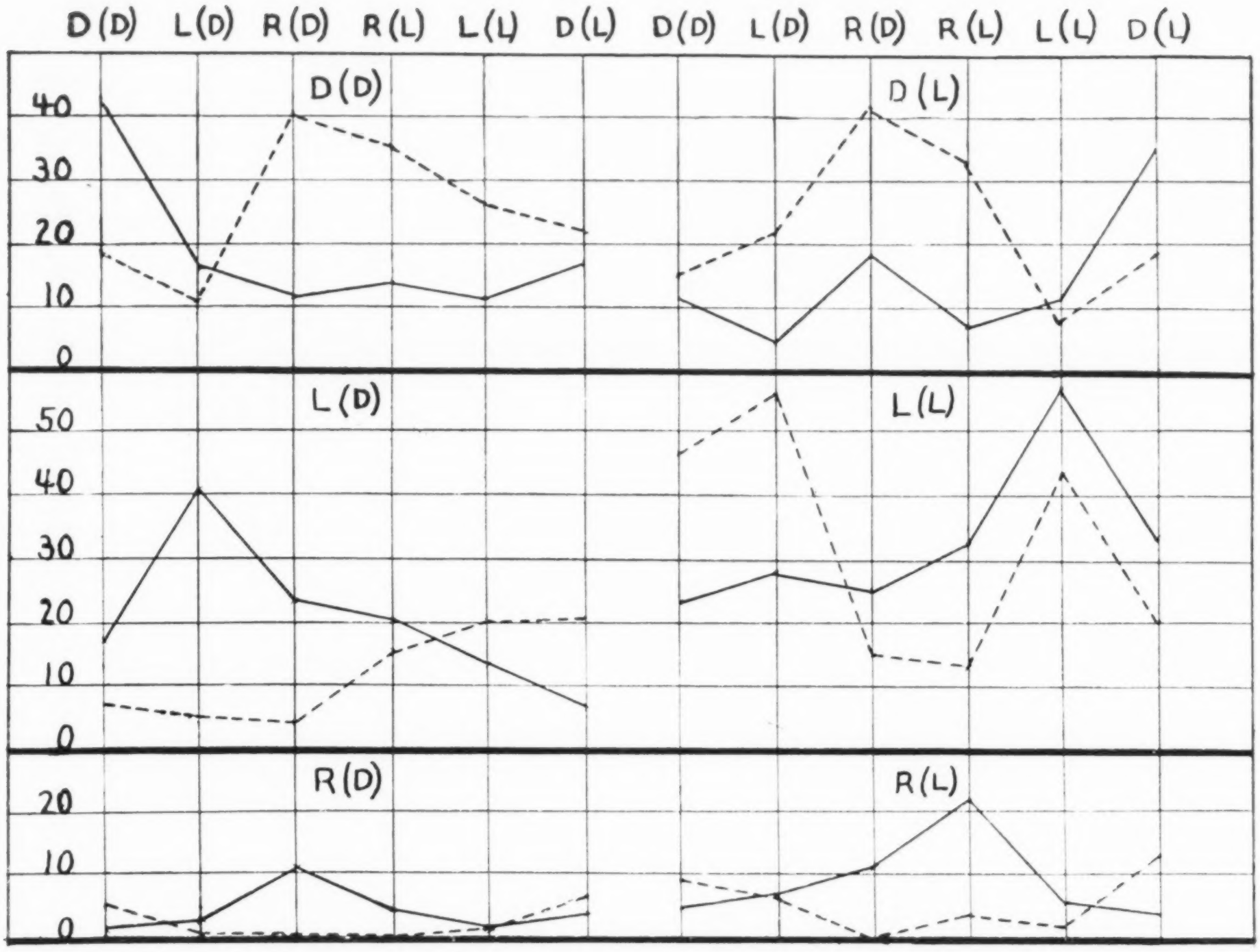
Of more interest than the heredity of these unusual traits is that of the common variations in skin, hair, and eye color. Unfortunately the problems are much more difficult. When even such an uncommon color as red hair occurs in two relatives one can have no such assurance that the same factor is

[7] Castle, W. E., and W. E. Farabee, 1903, *Sci. N. S.*, 17.

[8] Davenport, C. B., and G. C. Davenport, 1910, *Amer. Nat.*, 44:705-731. 1916, Jour. Her. 7:221-223.

[9] Apert, 1914, Jour. Her., 5:492-497.

[10] Holmes, S. J., and H. M. Loomis, 1910, *Biol. Bull.*, 18:50-65.



HOW HAIR AND EYE COLOR ARE INHERITED

Solid line—per cent which those of each combination of hair and eyes color form of the relatives of the color combinations at the top of the figures. Broken line—per cent of those of each color combination form of the husbands and wives of the color combination at the top. D—dark hair, L—light hair, R—red, auburn or yellow hafr, (D)—dark eyes, (L)—light eyes. (Fig. 17)

responsible as in the case of traits which are peculiar to a few families. As noted, hair with sufficient suggestion of red to be called auburn is found in 8.8% of a random Wisconsin student population. If red were recessive this would mean that almost half the remaining population would be heterozygous. The situation is even more difficult to analyze in the case of the differences between dark and light hair or eyes, brunette or blond complexion, etc. Again, none of these common variations are obviously discontinuous. All grades of complexion between dark brunette and the fairest blond are common in persons of British descent. All variations in hair color between intense black through brown to flaxen and from black through the reddish blacks and auburns to clear red may be found in such a population.

EYE COLOR

Eye color shows more discontinuity than hair and skin color as there is rather of an abrupt transition between brown and eyes which show a distinctly greenish or bluish tint. Galton[11] considered human eye color a good example of discontinuous heredity. Nevertheless it appears that the discontinuity is superficial even here. Eye color is due to pigment deposited on both sides of the iris. There is also pigment in other parts of the eye, including the retina. In a series of eyes showing gradual reduction in pigmentation, the

[11]Galton, F., 1889, "Natural Inheritance."

granules disappear first in front part of the iris. With pigment on the back, but not on the front, the effect is blue. A bluish or greenish appearance comes in rather abruptly when the anterior pigment is reduced to a certain point. With further reduction of the quantity of pigment the iris becomes a pale gray blue as in albinos, and the parallel reduction in the retina reaches a point at which vision is impaired and a red reflex becomes visible through the pupil.

Hurst[12] and Davenport,[13] working independently, arrived at the conclusion that dark eye colors are dominant over the lighter colors. Hurst drew the line so as to include only the purest blues in the recessive class, considering presence and absence of pigment on the part of the iris as the opposed characters. Davenport drew no such sharp line, but concluded that any darker color was dominant over any lighter color. He recognized that the results were not wholly clear-cut and that complications must exist. Holmes and Loomis[14] were more doubtful as to the value of the Mendelian description. They found that the darker colors tended to be dominant over the lighter ones, but that inheritance often seems blending and that offspring might be darker than either parent.

Hurst based his conclusions on data from a single village in Leicestershire. As the data show that there is no appreciable assortative mating for eye color, the population may be assumed to be in equilibrium. A good test of the unit factor hypothesis can be made by considering the proportions of the different classes in such a population. Such a test applied to data in shorthorn cattle, in an earlier paper, pointed overwhelmingly to the unit factor hypothesis. In this present case, however, the result is not so favorable. The data are summarized below. By

Parents	Matings	Children		Expected children	
		Duplex	Simplex	Duplex	Simplex
Duplex x Duplex.....	50	240	18	221	37
Duplex x Simplex.....	69	187	137	201	123
Simplex x Simplex.....	20	0	101	0	101
	139	427	256		

duplex, Hurst means an eye with pigment on both sides of the iris, by simplex one with only posterior pigment—*i. e.*, a clear blue eye.

Among the children 37.5% are simplex. Among the parents 39.2%. The number of children from matings of simplex by simplex with random mating should be .375 x .375 or 14.1%. The actual number is 14.8%. The number from matings of simplex by duplex should be 2 x .375 x .625 or 46.9%. The actual number is 47.4%. There is, evidently, no appreciable assortative mating. As the number of heterozygous dominants must be twice the product of the square roots of the homozygous classes in a population which is in equilibrium, and is without assortative mating, we can deduce the number of the two kinds of dominants. Where x^2 is the proportion of recessive (37.5%), the proportion of homozygous dominants must be $(1-x)^2$, which equals 15.0%, and the proportion of heterozygous dominants must be 47.5%. From these figures, the number of simplex children which should be produced by each type of mating may be calculated. Thus duplex by duplex should produce 37 simplex children, much in excess of the number found (18)

[12]Hurst, C. C., 1908, *Proc. Roy. Soc. B.*, 80:85-96.
[13]Davenport, C. B., and G. C. Davenport, 1907, *Sci. N. S.*, 26:589-592.
[14]Holmes and Loomis, *loc. cit.*

while duplex by simplex should produce 123 simplex children considerably in defect of the number found (137). The discrepancies are so great that it must be concluded that some more complicated explanation must be adopted than that of a single unit factor.

In addition to the evidence above is the evidence that light eyed parents may have children with darker eyes than their own. There are a number of such cases in Davenport's data. Holmes and Loomis have several cases including one in which two blue-eyed parents had a brown-eyed child. The writer knows personally of two distinct cases. Summing up, we may say that the factor or factors for light eyes have somewhat more tendency to be recessive than dominant, but we cannot affirm that a single unit factor is the principal cause of differences.

HAIR COLOR

Turning to hair color, we find a similarly unsatisfactory situation from the Mendelian standpoint. Davenport[15] classifies variations in hair color into two independent groups. He considers the granular pigment of black and brown hair as wholly distinct, physiologically and genetically, from the diffuse red pigment of clear red hair. He holds that these two kinds of pigment can be mixed in any proportions. In the presence of the granular pigment the color is black regardless of whether diffuse pigment is present or absent. Diffuse pigment in the absence of granular pigment is responsible for red, while with both pigments absent, or nearly so, the color is white to flaxen. The relations may be represented in the following scheme in which intermediate colors have been introduced. Variations in amount of granular pigment are represented horizontally; variations in amount of diffuse pigment vertically:

Black	Reddish-brown	Red
Black	Yellow-brown	Yellow
Black	Brown	Flaxen

Objections can be raised to this scheme on theoretical grounds, based on our present knowledge of the relations of the colors in other mammals. In guinea-pigs, for example, we have black granules and diffuse red pigment (as well as red granules), which one can hardly doubt are closely similar to the human pigments.[16] In guinea-pigs, however, it is certain that red and black cannot be treated as independent physiologically. The same factors for piebald (class 1a) inhibit both colors in spots in the fur; factors in the albino series (class 1b) dilute both colors, while factors of class 2a, as the tortoise shell and agouti factors, may replace a black, which is unassociated with red pigment, by intense red. These statements hold good for factors in classes 1a, 1b, and 2a in all other mammals which have been discussed. However, it will be shown that a scheme which differs only in theory from that above may be devised, which is in harmony with the relations of black and red in other mammals.

Davenport concluded, from a study of pedigrees, that the more intense condition of either pigment is dominant over the less intense. He gives abundant evidence that the lighter colors may be transmitted by dark haired persons. As in the case of eye color, however, we find rather numerous cases which do not fit the theory. Thus in one family, in Davenport's tables, flaxen by light brown produced red. In two cases, two light brown parents produced either auburn or red-haired children. In these cases, the children seem to have had more red pigment than either parent. Cases in which the children had more dark pigment than either parent are even more abundant, especially when we compare grandparents and parents in the table. It is not surprising, on any theory, that young children should seldom be darker than their parents, as the full intensity of hair color is not reached until maturity. In Davenport's tables we find two light brown parents producing dark or black-haired children in several cases. We find that red by red may produce black. In one remarkable case light

[15] Davenport, C. B., and G. C. Davenport, 1909, *Amer. Nat.*, 43:193-211.
[16] Hunt, H. R., and S. Wright, 1918, Jour. Her., 9:178-181.

brown by very light red produced the extremes of hair color—jet black and albino. Holmes and Loomis noted several cases in their records similar to those above, and many such cases can be found in the data of Pearson, Nettleship, and Usher. From all of these sources we get abundant evidence of segregation of some sort. It is clear, however, that if there is one main factor by which red and light brown differ from black, it must be imperfectly dominant, and that there must be other factors which raise or lower the pigmentation of the heterozygotes from one extreme to the other.

SKIN COLOR

With skin color the difficulties in study are naturally greater than with either eyes or hair color. As in the other cases, Davenport[17] concludes that the darker shades tend to be dominant over the lighter ones. Where wide crosses are made, as in the union of white with negro, it is well known that there is not unit Mendelian inheritance. The mulattoes are intermediate in color and their children are still mulattoes. Davenport has found, however, that there is much variability in the second generation, and that the results can be explained on the basis of two pairs of Mendelian factors, both imperfectly dominant. Here, again, it is impossible to speak of particular Mendelian factors as demonstrated. We can merely say that there is evidence for Mendelian segregation of some sort, and that the number of factors which need be hypothecated is not very great.

CORRELATED VARIATION

So far we have dealt with hair, skin, and eye color as wholly separate characters. In each case, we have been forced to conclude that the evidence has not demonstrated satisfactorily the existence of particular unit factors with clearly defined effects, but merely the presence of Mendelian segregation of a complex kind, with dominance tending toward the darker types, but probably imperfect as a rule. This is practically the conclusion reached by Holmes and Loomis in their study of hair and eye color, and, indeed, has been recognized, more or less, by all workers in this difficult field. But even if we were able to grant that the main effects are due to single pairs of unit factors in each case (considering only dark granular pigment), we would find great difficulty in accounting for the relations of these characters to each other. The three factors for dark hair, dark eyes, and dark skin, respectively, must either be identical or independent of each other. If identical, correlation in hair, skin, and eye color should be nearly perfect. If independent there should be no correlation, unless the population is one in which there is assortative mating. With partial linkage of factors, the correlations would still be zero. It would merely require a longer time for a heterogeneous population to reach equilibrium.

It is common experience that blue eyes tend to go with light hair and a fair skin. The degree of correlation, however, is far too low to harmonize with the hypothesis that there is merely one series of factors for all melanic pigmentation. Pearson[18] has calculated the correlations between hair and eye color in data from several nations with the following results:

Sweden (conscripts)	.259
Prussian (school children)	.271
Italy (conscripts)	.309
German Jew (school children)	.338
Baden (conscripts)	.354
Great Britain (school children)	.420

The correlations are so low that they might be suspected to be the result merely of racial heterogeneity. A correlation table involving all Europe would thus show a very high correlation simply because dark-haired, dark-eyed Spaniards and fair-haired, blue-eyed Scandinavians do not intermarry. It might be an accident from a physiological standpoint that both dilution of hair color and of eye color have become associated in the Scandinavian people.

[17] Davenport, C. B., 1913; Carn. Inst. Wash. Pub. No. 188, 1914, Jour. Her., 5:555-560.
[18] Pearson, K., 1904, *Biom.*, 3:459.

It can be shown, however, that there is a real physiological correlation from other data. The evidence from the data of Holmes and Loomis will serve as an example.

This data were obtained from students at the University of Wisconsin. In 71 families fairly complete records of hair and eye color were obtained for all brothers and sisters, parents, and grandparents. The authors' conclusions have already been noted briefly. The data are worthy of further analysis. For the present purpose eye color is conveniently divided into two classes—dark and light. The division is made at the point at which a bluish or greenish tint is obviously present. Black, brown, light brown, and hazel are called dark, while green brown, gray, and blue are called light. Hair color is classified as dark, light, or red. By dark is meant only black in adults, but both black and dark brown in children. This compensates, in part, for the great change with age. The category red is made as wide as possible, including auburn, chestnut, and a few yellows, as well as dark and light reds. Even thus it includes only 59 individuals or 8.8%. The tables are based on 364 adults (parents and grandparents), and 305 children. Among the adults 136 are dark haired, 200 light haired, and 28 red haired. Among the children these classes number 81, 193, and 31, respectively. The adult males do not differ appreciably from the females in hair color, but have slightly lighter eyes (68% light in males, 58% in the females).

TABLE 1.—*Per Cent of Light Eyes Associated with Each Hair Color*

Hair	Adults	Children
Dark	41	42
Light	76	64
Red	75	68

Dark-haired persons clearly have light eyes much less frequently than do light or red-haired persons. That this is not due to assortative mating such as would be the case if the students came in part from Italian, in part from Scandinavian families, is shown by Table 2, in which the percentage of husbands and wives of those with the different hair and eye colors are given for each hair and eye color.

TABLE 2.—*Association of Hair and Eye Colors in Husbands and Wives by Per Cent.*

	Hair			Eyes	
	Dark	Light	Red	Dark	Light
Dark hair	41	46	13	33	67
Light hair	31	65	4	38	62
Red hair	64	29	7	54	46
Dark eyes	33	56	11	30	70
Light eyes	40	55	6	42	58
Average	37	55	8	37	63

Persons with dark hair showed some preference above the average for their own color, but also for red hair and for light eyes. Persons with light hair preferred their own hair color, but showed no marked preference in eye color. Those with red hair show a very marked preference for black hair and also for black eyes. Dark-eyed persons showed little preference in hair color, but chose light-eyed mates considerably in excess of the average. The converse of the last statement is true of light eyed persons. While the numbers are too small in most of these cases to attribute much significance to them, it is at least clear that there is no assortative mating which can account for the correlation between hair and eye color found in individuals. There can be no question that light hair is connected physiologically with light eyes. In the case of red hair, the difference between 72% light eyes among 59 red-haired persons and 41% light eyes among 227 dark-haired persons is significant and not due to assortative mating.

This conclusion that hair, eye, and also doubtless skin color are physiologically connected, finds abundant analogies in the lower mammals. Indeed we have found it to be the rule that dilution factors of any kind (as opposed to pattern factors) produce their effect

wherever there is pigment of the proper kind. Thus in such mammals as the guinea-pig in which at least three independent sets of factors dilute hair, skin, and eye color, it has been found necessary to consider simultaneously all of the effects of any factor in order to analyze the heredity. It would seem desirable to apply this method to human data. The data of Holmes and Loomis is admirably adapted to this purpose.

COMBINATIONS OF HAIR AND EYE COLOR CONSIDERED AS UNITS

Let us then consider as distinct color varieties, the six combinations of hair and eye color—dark, light, and red hair each with dark or light eyes, and investigate their relations. Tables in which grandparents and parents are compared together, parents and offspring, and offspring with each other give fairly consistent results. By combining all of the data into one table, however, the results are brought out more clearly, freed from some of the irregularities due to small numbers. The fact that both parental and fraternal correlations are usually about the same, viz., .50 for characters which are wholly genetic, will serve as a justification for this procedure. In making up the table, parents and offspring were entered in both subject and relative classes. In order that the fraternal correlation should not be given undue importance, each entry was weighted inversely as the size of the sibship. The usual method of making fraternal correlations gives a family of 15 a weight of 210, where a family of 2 has a weight of only 2. It seems fairer to weight a family according to the number of brothers of a random individual and so give these families weights of 14 and 1, or 28 and 2 after doubling to make comparable with the double entries in the parent-offspring correlations. It may be said in passing that the unmodified fraternal correlation brings out the same relations as those presented below, even more clearly. The relations are most clearly brought out by calculating the per cent of cases in which each color combination occurs in relatives of each kind. (Table 3.)

Thus by reading down a vertical column we find that light hair with dark eyes was the color combination of 17.0% of the relatives of brunettes, of 40.9% of the relatives of others with light hear and dark eyes, etc. In the tables D(L) means dark hair with light eyes, R(D) red hair with dark eyes, etc.

The high degree of heredity of each combination is the first thing which is revealed by this table. This point, however, shows that before going farther it will be well to examine the data for assortative mating. If light eyed red haired persons have a special preference for another color some evidence for which we have already noted, this color should be in excess among relatives, as well as red hair with light eyes. Table 4 gives the per cent of cases in which those of each color combination married persons with the same and the other combinations. This table gives some idea of marriage prefer-

TABLE 3.—*Per cent of the different color combinations among relatives of those with each color combination (reading horizontally). For measurement of degree of association of one color combination with the others, read vertically. Based on 233 pairs of grandparents, with parent, 608 of parent with offspring and 242 random offspring with offspring. Each pair entered twice, making table symmetrical before calculation of per cents.*

	D(D)	L(D)	R(D)	R(L)	L(L)	D(L)	
D(D).....	41.7	17.0	1.6	4.7	23.5	11.7	100.2
L(D).....	16.8	40.9	3.1	6.8	27.9	4.5	100.0
R(D).....	11.7	23.3	10.7	10.7	24.9	18.6	99.9
R(L).....	13.9	20.5	4.3	21.9	32.3	7.0	99.9
L(L).....	11.3	13.6	1.6	5.2	57.3	11.0	100.0
D(L).....	17.1	6.7	3.7	3.4	33.6	35.5	100.0

ences, but more important from the standpoint of heredity is a similar table in which the marriages are weighted by the number of relatives in Table 3 connected with each. In Table 5 the marriages were weighted by the number of the children with an additional weight of one-third in the parental entries (as opposed to the grandparental) in order to balance approximately the fraternal correlation among the children in Table 3.

The results are presented graphically below. In these diagrams, the solid lines represent the per cent of cases in which a given combination is found in relatives of the various kinds, and the broken lines represent the similar percentages for matings (weighted).

NONASSORTATIVE MATING

The graphs on the whole tell a very consistent story. The heredity of the different combinations is obvious. In each of the cases those of a given combination form a larger per cent of the relatives of their own color than of any other. In a general way the colors fall into the order of relationship in which they are here arranged. Dark eyed dark, dark eyed light, dark eyed red, light eyed red, light eyed light with light eyed dark completing the cycle, showing relationship to dark eyed dark as well as light eyed light. A consideration of merely the correlation among relatives, however, gives a very imperfect idea of the connection between the colors. There is approximately at least equal transmission by the parents so that one would expect that the combination for which a given color shows most preference in marriage would also show preponderance among the children. But it happens to a surprising extent that the reverse is true. In general these people seem to have preferred to marry those of the color combination most remote from their own, so that where the line of preferential mating is depressed the line of relatives is elevated and the reverse. In order to give a rough measure of the nonassortative mating, the rank of frequency as a husband or wife was tabulated against the rank of frequency as a relative for each color in connection with each color. This means that rank in the vertical column in Table 3 was correlated with

TABLE 4.—*Per cent of marriages of each kind made by each kind of individual (reading horizontally). For measurement of degree of assortative mating (or reverse) read vertically. Based on* 182 *marriages.*

	D(D)	L(D)	R(D)	R(L)	L(L)	D(L)	
D(D).....	17.3	9.9	2.5	12.4	44.5	13.6	100.2
L(D).....	17.0	8.5	2.1	4.3	51.1	17.0	100.0
R(D).....	28.6	14.3	0.0	0.0	28.6	28.6	100.1
R(L).....	47.6	9.5	0.0	9.5	14.3	19.1	100.0
L(L).....	23.5	15.7	1.3	2.0	51.0	6.5	100.0
D(L).....	20.0	14.6	3.6	7.3	18.2	36.4	100.1

TABLE 5.—*Same as Table* 4, *except that the number of marriages of each kind is weighted by the number of cffsprings produced and the parental generation is given more weight than the grandparental. (See text.)*

	D(D)	L(D)	R(D)	R(L)	L(L)	D(L)	
D(D).....	18.2	7.0	4.5	9.0	46.6	14.8	100.1
L(D).....	10.8	4.9	0.7	6.0	55.9	21.7	100.0
R(D).....	40.1	3.9	0.0	0.0	14.4	41.6	100.0
R(L).....	35.5	15.4	0.0	3.4	12.5	33.1	99.9
L(L).....	26.0	20.2	0.9	1.8	43.5	7.6	100.0
D(L).....	21.8	20.7	6.9	12.4	20.0	18.4	100.2

rank in the vertical columns of table 4 or 5, making correlation Tables with 36 entries.

The correlation between rank among relatives and rank among husbands and wives is —.51 when the latter are weighted, —.28 when unweighted. The difference seems to be due largely to a smaller degree of nonassortative mating among the grandparents than among the parents. Where the matings are unweighted the grandparental matings are, of course, more important than the parental.

TWO KINDS OF DILUTION OF EYE COLOR

The results as to the connection between the different color varieties agree in the main with those to be expected on any theory. One would expect to find D(D) closer to either D(L) than to L(L), and D(L) closer to D(D) and L(L) than to L(D), whether hair and eyes are inherited independently or in part together. Perhaps the most important point which is brought out is the very low relationship of R(L) to D(L) and the high relationship to L(D). We have seen that there is a physiological relationship between red hair and light eyes. It seems necessary to suppose that the same factor which reduces the amount of black pigment in the hair and permits red to appear in its place, reduces black in the eyes. But we cannot suppose that factors of this class are responsible for the light eyes in black haired persons. Thus as a basis for classifying the color varieties it would seem to be a good working hypothesis to suppose that two fundamentally different kinds of dilution factors for eye color are at work. One also reduces black hair to red hair; the other has no such effect. Since, however, both D(L) and R(L) are quite closely related to L(L), we may go a step farther and suppose that the same factors which reduce D(D) to D(L) reduce R(L) to L(L). These relations may be indicated briefly as follows:

D(D) R(L)
D(L) L(L)

Let us compare the effects of these hypothetical factors with the classes of color factors found in mammals. A factor which reduces red to flaxen or white, in extreme cases, must be placed in class 1b with the albino series in the lower mammals. These are factors which are supposed to reduce the amount of the fundamental enzyme for color production (enzyme I). Such factors should produce a dilution of black pigment in hair and eyes as well as of red in the hair, but the dilution should be very much less marked in the black hair. The other class of dilution factors—that which reduces D(D) to R(L) must be placed in $2a_3$ or 2b. Such factors produce a general reduction in quantity or strength of enzyme II, and leave enzyme I free to develop red pigment. A fairly close parallel can be taken from relations which the writer has found to hold in guinea-pigs. The albino series of four alleomorphs C, C_d, C_r, and C_a may be taken to represent class 1b, *i. e.*, general pigment dilution. The pair extension of black (E) and restriction of black (e) of class $2a_2$ may be taken to illustrate a factor which replaces black by red. The parallel is not complete here, as factors E and e belong to a series in which an intermediate allelomorph E_p produces tortoise shell. The series changes black to red by way of a pattern of spots, eyes remaining unaffected, instead of by way of a general dilution which may be expected to affect the eyes.

The colors called dark and light sepia in guinea-pigs in the earlier papers are here called black and dark brown, the human hair colors which they match. The dark sepia of C_dC_d, C_dC_r, and C_rC_r is, as a rule, sufficiently browner than the black of C— to be distinguishable but is fully as black as the average black hair in Europeans. The light sepia of C_rC_r and C_rC_a is light only by comparison with dark sepia. Typical samples match very closely human hair which would be called dark brown. It will be seen that the arrangement of hair colors suggested for man is the same for the common colors as that adopted by Davenport, but the theoretical interpretation is quite different and brings the eye colors into the same scheme.

	Guinea-pigs		Man			
	EE	ee				
C	Black (B)	Red (B)	B(B)	Au(Br)	R(Blue)	R(Blue)
C_dC_d	Black (B)	Yellow (B)				
C_dC_r	Black (B)	Cream (B)	B(Br)	Br(Br)	Y(Blue)	Y(Alb)
C_dC_a	Dark Brown (B)	Cream (B)				
C_rC_r	Black (Red)	White (Red)	B(Blue)	Br(Blue)	W(Blue)	W(Alb)
C_rC_a	Dark Brown (Red)	White (Red)				
C_aC_a	Sooty White (Pink)	White (Pink)	W(Alb)	W(Alb)	W(Alb)	W(Alb)

B, Au, R, Br, Y, and W stand for black, auburn, red, brown, yellow and white hair respectively (B) (Br) and (Alb) stand for black, brown and albinotic eyes.

Instead of supposing that the factors by which black differs from red determine the presence of a granular pigment wholly independent of a red, we suppose that an additional enzyme (enzyme II) is determined which converts the fundamental enzyme, which alone produces red, to an enzyme which can produce black. The same effect is supposed to take place in the eyes and skin as in the hair. The change from white or flaxen to red is interpreted as being due to an increase in the fundamental enzyme (enzyme I) instead of the addition of diffuse red pigment wholly independent of black. As in the other mammals, we suppose the threshold for production of red (enzyme I acting alone) is at so much higher a level than the threshold for black (enzyme I assisted by enzyme II) that we find white or flaxen in place of red at a level at which we find black virtually unchanged.

We would expect to find effects of the factors $2a_3$ on the skin as well as in hair and eyes. The general correlation has been alluded to. In the case of red, Pearson has shown that freckling is especially characteristic of red haired persons.

ALBINISM, BLONDNESS, AND RED HAIR

The question now arises as to the position of albinism in this scheme. If we take the condition of the eyes—pale iris, red pupil, nystagmus, photophobia, and poor vision—as the fundamental criterion for albinism in man (rather than mere white hair), we see that such a condition may be reached by extreme variation along two routes. Extreme reduction of enzyme I should at length reduce the blue eyed black-haired type to a pale brown or even white with albinotic eyes, comparable to the albinos of rodents. Doubtless most of the albinos of dark races are of this type since the chances are that such a rare variation differs from the normal by only one factor. The evidence on the whole indicates that such albinism behaves as a unit recessive factor. Such albinism doubtless also exists in the white race, but is not easy to distinguish from the second kind. The second kind of albinism we find in Pearson's red and yellow haired albinos which suggest extreme reduction of enzyme II, rather than of enzyme I.

These red and yellow haired albinos, however, appear to be very uncommon. But the observation of Davenport and Pearson in regard to the unusual frequency of red haired persons among the relatives of albinos of the ordinary white haired kind suggests that we are here dealing with the combined effects of both kinds of variations. Thus variations of class $2a_3$, which alone may reduce black merely to a blue eyed red, only a little more extreme than usual, when associated with a grade of general dilution which will reduce red to white, but black eyed black merely to blue eyed black, should result in a blue eyed white type with more or less albinotic eyes. Such an albino would be closely comparable with the red-eyed white guinea-pigs (see C_rC_r).

The main difference is that such red eyed white guinea pigs have no more dilution of the eyes than red eyed black ones (EE C_r C_r), a point explained by the different character of the guinea-pig restriction factor (of class $2a_2$) and the human variation for red hair of class $2a_3$. The evidence does not yet warrant the acceptance of any unit factors for either of these kinds of variations in man, though there is much evidence of segregation. If we suppose that black is only imperfectly dominant over extreme reds (evidence for which has already been noted) we can easily account for the numerous auburn and chestnut browns among the relatives of European albinos.

COLOR AND RACE

This leads to a consideration of the racial distribution of human color variations. Pearson and his collaborators have shown that dilute variations, probably of both kinds, occur occasionally in all or most of the dark-colored races. Dark hair with green eyes and reddish-brown hair with dark eyes are found as well as the more extreme albinotic types. Such variations could doubtless develop blond races, if given an advantage in selection. In most parts of the world, however, such variations with their lack of adaptation to excessive sunlight are rather selected against. In the foggy region of northern Europe, however, conditions are favorable. Here selections seems to have favored dilute variations of all kinds, probably largely through marriage. A traditional association of blondness with nobility or racial preeminence would lead to such a result. Around the shores of the Baltic and the North Sea we find typically blue-eyed, flaxen haired people, who, we must suppose, possess variations of both classes 1b and $2a_3$ to a marked extent. Among the Lithuanians and certain of the Finnic peoples along the east shores of the Baltic (Livs, Esths, Tchouds) this blondism reaches its maximum according to Pearson, Ripley,[19] and others. The hair is described as white or yellowish white, and the eyes, very pale blue. In Scandinavia, North Germany, and parts of Britain the same extreme blond type is common. Surrounding the area of extreme blondism we find a zone of segregating colors. Dark hair with blue eyes and red hair with different eye colors occur quite frequently as well as the fully blond or brunette types. The British Isles, northern France, southern Germany, and northern Russia are in this zone, and also the more remote parts of the world settled by descendants of these people. The data of Holmes and Loomis from Wisconsin is a good example of this zone. Outside of this zone of segregation, in Europe, are the typically brunette populations of Southern and southeastern Europe and Asia.

We have treated both variations of class 1b and $2a_3$ as centering around the Baltic and fading out in all directions. There is some evidence, however, that the zones of frequency of the two kinds of variations are not quite concentric. Dark red hair, according to Ripley, is characteristic of the Finns away from the coast (*e. g.*, the Votiaks and Zyrians). It is common even in Western Siberia, as among the Voguls and Ostiaks. Ripley also says that some tinge of red is almost universal in the Russians of the north and is common in Hungary and parts of Austria. It thus seems probable that dilution factors of class $2a_3$ are distributed much farther to the east than those of class 1b. In the west of Europe, the two kinds of variation seem to fade out more nearly together so that both black hair with blue eyes and red hair are common throughout the British Isles. However, black hair with pale blue eyes is most characteristic of the Gaelic speaking portions of Scotland and Western Ireland. Ripley speaks of this combination as highly characteristic of the Bretons and it is even said to be not uncommon in Spain. Apparently variations of class 1b have somewhat the greater western spread.

A difficulty in this interpretation of

[19]Ripley, W. Z., 1899, "The Races of Europe," 624 pp.

blondness must be met. Among the dark races, variations which produce relatively little dilution of hair color are apt to produce photophobia, nystagmus, and imperfect vision. But these eye defects seem no more common in Scandinavia and the surrounding regions than elsewhere. It is, however, quite likely that with selection for blondness of the hair, there would be selection against the accompanying eye defects. An adjustment in regional differentiation may thus have been reached by which eyes come to be affected less than skin and hair by the dilution factors. There is also some evidence from Pearson's data that in Scandinavia and Northern Germany eye colors are relatively darker for any given hair color than in the surrounding countries. Flaxen hair with dark eyes seems to be quite common there, while very rare, for example, in Great Britain.

The discussion so far has neglected racial lines. The anthropologists are generally agreed that there are three main racial types in Europe. They hold that Europe was originally inhabited by dolichocephalic races related to those of northern Africa and southwestern Asia. At present only the fringe of Europe has such types in anything like purity. The heart of the continent from the Balkans to France is inhabited largely by brachicephalic people, believed to be derived from the highlands of central Asia where similar people still live, connected with the European type through the Armenians of Asia Minor. This so called Alpine race is typically dark in hair and eye where found presumably in the greatest purity in Asia and southeastern Europe.

The original dolichocephalic races of Europe had an immense time in which to become differentiated from each other. These differences are manifest in the dolichocephalic peoples living now around the fringe of Europe. Thus the inhabitants of Southern Italy, Spain, and Southern France of the Mediterranean race are dark and relatively short. Among the older races of the British Isles somewhat different from either the Mediterraneans or the Nordics, the inhabitants range from medium (in Wales) to the tallest in Europe, and all are especially angular featured according to Ripley, and are rather dark. The Scandinavians, North Germans, and Finns of the Nordic race are rather tall, less angular in features and very fair. It is clear that the dilute variations arose among the northern dolichocephalic people probably with somewhat different centers of dispersal for the two kinds of dilution, as noted before. Constant mixture with the dark Mediterraneans, Alpines, and Mongols produced the zone of segregating colors.

CONCLUSION.

In conclusion we may say that certain rare traits peculiar to families such as premature grayness, piebaldism, and albinism (in some families) follow easily determined rules of inheritance. Premature grayness and piebaldism behave as unit dominants. Piebald in some families is sex-limited. Albinism is in certain cases a unit recessive. The common variation of eye, hair, and skin color cannot yet be said to be completely analyzed. The most important variations seem to be of two kinds. First is general reduction of color (class 1b), affecting red pigment and eye color at a higher threshold than black of hair, but producing general albinism in extreme cases. Black hair with blue eyes is caused by moderate variation of this kind. Second is dilution of black only (class $2a_2$) which affects hair, skin, and eyes, and in extreme cases produces a red haired type of albino. Red hair with blue eyes is typical of moderate dilution of this type. Combinations of the two kinds of variation produce the blond types which pass into more or less perfect albinism much more easily than when either type of variation is alone.